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Point-Sampling Compared with Plot-Sampling in Southeast Texas

BY
L. R. GROSENBAUGH
W. S. STOVER

POINT-SAMPLING has long been a familiar technique in estimating forest acreage from a map or aerial photo. Recently, through the use of an angle-gauge[1] which inflates tree basal area on the ground by a constant factor, the point-sampling concept has been extended to estimates of tree volume and tree frequency per acre,[2] as well as to tree basal area per acre. Although various angle-gauges have been devised, the one with the most promise is a simple wedge-prism,[3] which can be elaborated to allow for slope-compensation and magnification.[4] The development and application of point-sampling theory as applied to trees has been summarized in a recent publication.[5]

Trees may be visualized as being surrounded by imaginary rings, with each ring diameter being a constant (K) times tree diameter, and each ring area being a constant (K^2) times tree basal area. Sample trees from the specified population are selected by locating a point at random within the population bounds and then making complete sample measurement of any and all trees whose rings lap over the sampling point. It is convenient to use an angle-gauge to decide which trees have rings lapping over the sampling point. Sample trees must have trunks which subtend larger horizontal angles at breast height than the angle-gauge when all angle vertices are directly above the sampling point. K^2 is then a function of the angle θ used as a gauge, thus,

$$K^2 = \csc^2\left(\frac{\theta}{2}\right) = 1 + \cot^2\left(\frac{\theta}{2}\right) = \frac{1}{\text{haversin } \theta} = \frac{2}{1 - \cos \theta}$$

If individual tree basal area (or BA)

[1]Bitterlich, W. 1948. Die Winkelzählprobe. Allg. Forst- u. Holzw. Ztg. 59(1/2): 4-5.

[2]Grosenbaugh, L. R. 1952. Plotless timber estimates—new, fast, easy. J. For. 50: 32-37.

[3]Müller, G. 1953. Das Baumzählrohr. Allgemeine Forstzeitung 64 (19/20): 249-251.

[4]Bruce, D. 1955. A new way to look at trees. J. For. 53: 163-167.

[5]Grosenbaugh, L. R. 1955. Better diagnosis and prescription in southern forest management. U. S. Forest Serv. S. For. Exp. Sta. Occ. Pap. 145, 27 pp.

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be expressed in square feet, and land area (or LA) containing the tree population be expressed in acres, each tree in the population has a definite probability of being sampled (by a single random point) which can be expressed as $\frac{K^2(BA)}{43{,}560(LA)}$. After a sample has been drawn, the presample probability of each sample tree's inclusion in the sample can be readily calculated; population totals for any desired variable can then be estimated by summing individual sample values of the desired variable divided by corresponding individual probabilities of being drawn, in accordance with sampling theory where samples have unequal chances of being drawn (i.e., p.p.s. sampling).

Thus if M trees have been selected by a single random point-sample, and if some variable quantity X associated with each tree is measured, as well as the BA of each, the sample-based estimate for the total of X in the specified land area or population is:

$$\frac{43{,}560\ (LA)}{K^2} \sum^{M} \frac{X}{BA}$$

The *per acre* estimate is the above divided by LA, or:

$$\frac{43{,}560}{K^2} \sum^{M} \frac{X}{BA}$$

If X should represent present tree basal area, then the expression simplifies to $\frac{43{,}560\ M}{K^2}$, and each individual sample tree basal area never need be measured. If X should be tree frequency, volume, past basal area, etc., then the summed ratios are not constant, and individual tree present basal area must be measured, along with each X.

This theory can easily be extended to include multiple sampling points, sloping terrain, etc.

It can be seen that the above procedure is merely a specialized adaptation of sampling with probability proportional to size (p.p.s.), familiar to all who have ever point-sampled or counted dots on a map or aerial picture. In general, p.p.s. sampling should be employed *with replacement* to avoid bias. Thus multiple sampling of the same tree does not involve bias, but failure to replace sample trees in the population might involve bias, although often the bias would be negligible.

Because of the fundamental difference between plot-sampling (where probability of tree selection is proportional to tree frequency) and point-sampling (where probability of tree selection is proportional to tree basal area), many people have tried to evaluate point-sampling by comparing it with complete enumeration on a small tract. Often such comparisons have been vitiated by improper calibration of the angle-gauge, use of volume/basal area ratios not based on the same tree volume figures that were used in complete enumeration, brush bias, edge-effect bias, biased treatment of doubtful trees, bias in locating sample points, misinterpretation of normal variation attributable to sampling, etc.

Sample Design and Field Procedures

The initiation of the U. S. Forest Service Forest Survey in 12 counties of southeast Texas in 1954 presented the Southern Forest Experiment Station with an excellent opportunity to validly compare means and precisions of point-sampling with those of plot-sampling. Care was taken to eliminate any of the above-mentioned sources of erroneous inference.

The counties were to be inventoried by standard Forest Survey plot procedure. Since in this area slope rarely exceeded 10 percent (at which a 1-percent correction factor is needed in point-sampling), it was decided to also select sample trees with a simple 104.18 minute wedge-prism (3.03 prism-diopters) by observation from the center of each ¼-acre circular plot on which regular Forest Survey data were taken. Both sets of data would later be pro-

cessed by punched card techniques; then basal area, cubic-foot, and board-foot density figures for each plot and concentric point-sample could be compared and analyzed. Since field crews could not work up tally sheets manually, they were unaware of the outcome of the check until long after field work was completed.

Essentially, Forest Survey procedure in southeast Texas involved obtaining a pair of ¼-acre plots (5-chain separation) at each intersection of a square grid (3-mile separation) falling on forested land. Although full Forest Survey data were taken on both plots (known as the principal plot and the auxiliary plot), the bulk of the comparisons and analyses discussed below are based on only the 655 principal plots obtained, with their concentric point-samples, in the 12 Texas counties inventoried in 1954–55. Basal areas on the 655 auxiliary points were worked up for a special analysis, however, so that an estimate of "within location" and "between location" variances could furnish a clue to possible changes in design of future surveys using point-samples.

Rather than have several crews use wedge-prisms with basal-area factors which differed, it was considered preferable to procure a large number of commercial 3-diopter wedge-prisms and select only those whose deviation as measured by several people and with two target sizes (3.03 inches and 9.09 inches) averaged 104.18 minutes or 3.03 diopters. Calibration (except that two target sizes were used) followed the procedure outlined in the reference cited in footnote 5. Any prism whose mean basal area factor lay between 9.9 and 10.1 was accepted, and all others were discarded. In effect, this allowed the basal area factor 10.0 to be used for every prism, with less than 1 percent maximum instrumental error. Three prisms meeting the above standards were found out of a dozen 3-diopter prisms calibrated. The "doubtful tree" check described below practically eliminated any remaining instrumental error, and also removed personal bias when borderline trees were encountered.

Any tree viewed through the prism which could not be clearly classed as "tally" (overlapping image) or "non-tally" (separated image) was checked by measurement. If distance to the tree (in feet and tenths) was *less* than 2.75 times tree d.b.h. (in inches and tenths), the doubtful tree was tallied. This 2.75 was the "plot radius factor" appropriate to the prism used; theory and application are discussed in the references cited in footnotes 2 and 5.

On the Survey, detailed sample-tree measurements (to the nearest tenth-inch of diameter) were taken for all trees lying in the quarter-acre plot and having d.b.h. larger than 6.95 inches. On a concentric 1/40-acre plot, trees with d.b.h. from 4.95 to 6.95 were measured to the nearest tenth-inch and trees with d.b.h. in the 2-inch intervals from .95 to 2.95 inches, and from 2.95 to 4.95 inches were tallied by frequency only (these will henceforth be referred to as 1 to 3 and 3 to 5–inch classes). The point-sample, however, included all trees larger than 1 inch in diameter.

In order to remove as much bias as possible from the 1/40-acre plot-estimate of the basal area in small trees in the nominal 2-inch and 4-inch classes, the senior author devised a technique using the ratio of two integrals (that of the basal area distribution over that of the frequency distribution). The technique is described in detail in the Appendix. It resulted in lowering the plot-estimate of basal area per acre nearly 1 square foot, as compared to what would have been obtained by the conventional biased technique of assuming that the basal area of the tree at the class mid-diameter is the same as the tree of mean basal area. This indicates the magnitude of bias which may be injected by neglecting grouping error in basal-area estimates.

Gross cubic-foot volumes (excluding bark but including cull) to a merchantable top diameter of not less than 4.0 inches inside bark were calculated for all trees in

TABLE 1. Comparison of means, standard deviations, and standard errors obtained for several variables on 655 forested locations in southeast Texas point-sampled by 104.18 minute prism (Method A) at center of standard one-quarter-acre circular plot (Method B).

BASAL-AREA COMPARISON

Sampling technique	Basal area per acre: All trees larger than 1 inch d.b.h. Mean	St. error	St. dev.	Probability that greater difference in means might occur by chance in sampling zero-difference populations
		Sq. ft.		
Point-sample (A)	53.76	1.49	38.2	$\frac{.041}{.727} = .056 = t_{.955}$
Plot-sample (B)	53.80	1.25	32.0	
Difference (A–B)	—.041	.727	18.6	95 percent probability

CUBIC-VOLUME COMPARISON

	Gross cu. vol. per acre: All trees larger than 5 inches d.b.h. Mean	St. error	St. dev.	Probability that greater difference in means might occur by chance in sampling zero-difference populations
		Cu. ft.		
Point-sample (A)	692.1	25.9	662.9	$\frac{.4}{10.7} = .037 = t_{.970}$
Plot-sample (B)	691.7	23.6	603.4	
Difference (A–B)	+.4	10.7	273.3	97 percent probability

BOARD-FOOT COMPARISON

	Gross board-foot volume per acre: All trees larger than 11 inches d.b.h. plus 9–11 inch conifers Mean	St. error	St. dev.	Probability that greater difference in means might occur by chance in sampling zero-difference populations
		Bd. ft.		
Point-sample (A)	3260	150.	3848	$\frac{37.}{59.4} = .622 = t_{.534}$
Plot-sample (B)	3297	143.	3663	
Difference (A–B)	—37	59.4	1522	53 percent probability

the sample with a d.b.h. larger than 4.95 inches. Standard Forest Survey volume tables (entered with d.b.h. to nearest inch, merchantable height to nearest 8 feet, and Girard form-class) were used for plot-sampled trees, and the same volume tables were used to derive volume/basal area ratios for point-sampled trees.

Gross board-foot volumes (excluding bark but including cull) to a merchantable top diameter (not less than 6.0 inches inside bark for conifers and 8.0 inches for others) were calculated for all conifers with d.b.h. larger than 8.95 inches and all hardwoods with d.b.h. of more than 10.95 inches. Standard Forest Survey volume tables (International log rule, with ¼-inch kerf) were used with the same entering variables as in the case of cubic feet. Ratios of board-foot volume to basal area were also derived for point-sampled trees as has been discussed above.

Results

In general, the comparison of point-sampling estimates with plot-sampling estimates substantiated what might have been expected from any well-conducted comparison of two unbiased sampling methods. No greater differences in mean basal area, cubic-foot volume, or board-foot volume per acre were observed than those which

might easily be attributed to chance or sampling variation. Although sampling with a systematic square grid complicates estimates of error, random-sampling formulas have been employed since evidence seems to indicate that errors of differences and ratios thus calculated will be on the conservative side.

As can be seen from the per-acre comparisons in Table 1, the point-sample estimate was .041 sq. ft. per acre lower in basal area, .4 cubic feet per acre higher in cubic-foot volume, and 37 board feet per acre lower in board-foot volume than the plot-sample estimate, where there were 655 points each in the center of the same number of ¼-acre plots scattered all over southeast Texas. When compared with appropriate standard errors of the difference, none of these approached the 5 percent level of significance—indeed, larger differences would have arisen more than half the time merely from sampling variation. Table 1 also gives standard deviations and standard errors for each type of sample—although the point-sample errors were slightly higher, the work involved was far less. Comparative times needed by each technique were not obtained in this preliminary test, so the relative efficiency of the two methods cannot be stated precisely.

Despite the fact that Table 1 indicates that 20 percent more point-samples are needed to give the same accuracy in cubic volume that plot-samples give—$\left(\frac{25.9}{23.6}\right)^2 = 1.20$—the tally-time for a single point-sample is much less than for a combined quarter-acre and fortieth-acre plot-sample (only 7,012 sample trees tallied on 1,310 point-samples, as compared to 28,510 sample trees tallied on 1,310 plot-samples; also, there are considerably fewer distance determinations needed in point-sampling). Efficient cluster-sample design would result in taking more point-samples than plot-samples at a location, which would still further diminish the 20 percent differential in needed locations.

Again, it is more feasible to use cheap one-man crews with point-sampling than with plot-sampling. Furthermore, point-sampling intensifies sampling of the larger, more valuable, and more variable board foot component at any given level of cubic foot sampling accuracy. This is because the 104.18 minute angle-gauge samples trees larger than 21.4 inches in d.b.h. more heavily and smaller trees less heavily than does the quarter-acre plot. Finally, field work and office compilation of growth estimates (along with related estimates of error) are expected to be considerably cheaper for the point-sample than for the plot-sample.

Although no numerical assessment of the advantages mentioned was made in this study, the authors feel that it is merely a question of the magnitude of point-sampling's superiority. Possibly an angle-gauge with a factor higher than 10 may prove more efficient under certain conditions; no attempt was made to study this or comparative costs, since such information can be ascertained by far less expensive methods than those employing regular Forest Survey crews.

Table 2 gives the same standard deviations and standard errors shown in Table 1, but expresses them as a percent of the mean. Here it is apparent that the differences indicated in Table 1 and mentioned above are very small: point-sampling was only 0.1 percent lower in basal area per acre, 0.1 percent higher in cubic-foot volume per acre, and 1.1 percent lower in board-foot volume. The coefficients of variation for point-sampling were slightly higher than those for quarter-acre plot-sampling—from 7 to 12 percent higher depending on whether board feet, cubic feet, or basal area is involved. Standard errors by either method were within 0.5 percent of each other.

It is interesting to note the correlation between the quarter-acre plot observations and the concentric 104.18-minute point-sample observations. Correlation coefficients are .874, .911, and .919 for basal

TABLE 2. Comparison of coefficients of variation and correlation, actual percentage differences, and percentage standard errors for several east Texas variables point-sampled by 104.18 minute prism (Method A) at center of standard one-quarter acre circular plot (Method B).

Variables sampled	Coefficient of variation: For (A): point method	For (B): plot method	For (A/B)[1]	Coefficient of correlation between plot and point	Actual difference: $\frac{\text{mean A}}{\text{mean B}} - 1$	Standard error of mean A[1] / mean B	Standard error of mean A: point method	Standard error of mean B: plot method
	Percent						*Percent*	
Basal area	71	59	35	+.874	−.1	±1.4	±2.8	±2.3
Cubic volume	96	87	39	+.911	+.1	±1.6	±3.7	±3.4
Bd. ft. volume	118	111	47	+.919	−1.1	±1.8	±4.6	±4.3

[1]The standard error of a ratio of means can be approximated in percent as:

$$\frac{C_{A/B}}{\sqrt{N}} = \sqrt{\frac{C^2_A + C^2_B - 2r_{AB}C_AC_B}{N}}$$

Where C_A, C_B, and $C_{A/B}$ are coefficients of variation and r_{AB} is a coefficient of correlation between A and B. Where mean A equals mean B, then $C_{A/B}$ may be approximated by the standard deviation of the difference between A and B divided by the geometric mean of mean A and mean B.

area, cubic-foot volume, and board-foot volume respectively. Although these are relatively high, as might be expected, the ratio of a point estimate to its surrounding plot estimate may vary from unity by 35, 39, or 47 percent about 1 time out of 3 (see coefficient of variation for A/B). The coefficients of variation and correlation can be related to one another and to the standard error of the ratio (point mean/plot mean) by the formula set forth at the foot of Table 2.

Before discussing frequency tables and comparisons of the methods at various density levels, it seems desirable to bring out certain underlying facts about ¼- and 1/40-acre plots and concentric 104.18-minute point-samples. Use of a 104.18-minute angle-gauge where all trees are exactly 21.4 inches in d.b.h. is equivalent to taking a ¼-acre plot (where all trees were exactly 6.8 inches in d.b.h., it would be equivalent to taking a 1/40-acre plot). Thus where trees tend to an average size smaller than 21.4 inches in d.b.h. (as they usually do in southeast Texas), the angle-gauge will tend to sample only some interior part of the ¼-acre plot, even though it may tally an occasional tree *larger* than 21.4 inches outside the ¼-acre plot. Similarly, the 104.18-minute point-sample will tally 1- to 5-inch trees on some interior part only of the 1/40-acre plot; it can *never* tally a 5-inch tree outside a 1/73-acre plot.

The situation, then, is analogous to enlarging a 1/40-acre plot to a concentric ¼-acre plot. Even though the *average* of the two estimates tends to be the same, extremes will occur much more frequently in the small plot. This is due to the patchy, clustered, or contagious nature of the density distribution. When a very high density is found on the small plot, enlarging the plot usually results in inclusion of density more nearly average. When a very low density is found on the small plot, enlarging it usually will also tend to include density more nearly average. Enlarging a small plot of nearly average density will tend to include areas of higher or lower density in more nearly equal proportions. As a rule, then, extremely high or low densities on small plots tend to regress to-

wards the population mean when the plot is expanded to larger size. Even though the frequency distribution of large-plot estimates of small plots is skewed at both high and low densities of small plots, both large and small plots furnish unbiased estimates of the *population* mean.

On the other hand, when a very high density is found on a large plot, a sample of a small part of it will not be in any way affected by the *population mean* outside the large plot. Instead, the small sample will tend to fall higher or lower than the large plot mean with nearly equal frequency (unless there is a badly skewed density distribution on the large plot). When a very low density (near but not quite zero) is found on a large plot, distribution is inevitably skewed, so a small plot will sample zero frequently, but occasionally it will hit a concentration much higher than the plot average. On the whole, the small plot tends to give an unbiased estimate of the large plot, and both tend to give an unbiased estimate of the population, as is well known.

A glance at Table 3 will indicate the pertinence of the above discussion, if point-sampling be regarded as the small-plot estimate of the ¼-acre plot. If a vertical column of frequencies is viewed, it illustrates what happens when point-samples (or small plots) are compared with their enlargement (¼-acre plots). When the points sample low density of basal area, the expanded plots surrounding them tend to include higher, more nearly mean density. If the points sample high density of basal area, the expanded plots tend to include lower, more nearly mean density. *This is not bias*, since the mean of the entire range of points tends to coincide with the population mean—it merely indicates that extremes of high or low density are much more frequent with points than with plots. The plot means are pulled toward the population mean more strongly than are the point means.

Now if a horizontal row of frequencies in Table 3 is viewed, it illustrates what happens when ¼-acre plots are sampled by points (or smaller plots). It will be noted that there is much less skew, except at the very lowest plot densities. In general, the point means are pulled toward the *plot* means, and are not much affected by the *population* mean.

Table 4 summarizes the *plot* frequency data horizontally from Table 3. It also provides comparisons of point and plot estimates of basal area, cubic-foot volume, and board-foot volume per acre by plot density classes (in this respect it merely breaks down the totals given in Table 1). Mean differences are tabulated by plot density class to show that they tend to be small when samples are numerous, and that their sign is not notably correlated with stand density.

In addition to this, Table 4 throws some light on how differences between point and plot estimates or ratios of $\frac{\text{point estimate}}{\text{plot estimate}}$ behave. It is noticeable that the variance of individual differences about zero tends to increase roughly as plot estimates increase, and that the variance of individual ratios about unity tends to decrease roughly as plot estimates increase (as long as at least 20 observations are available in a class). This is helpful in susbtantiating the hypothesis that $\frac{\Sigma \text{ point estimates}}{\Sigma \text{ plot estimates}}$ (or its reciprocal) would have furnished the best estimate of a correction ratio in case an instrumental or personal bias had caused the ratio to differ noticeably from 1.

If point-sample estimates be called Y, and plot-sample estimates be called X, and if it is desired to derive an average correction factor or ratio estimate $B = \frac{Y}{X}$, there are three common situations:

When $\left(\frac{Y}{X} - B\right)^2$ tends to get smaller in direct proportion as X^2 gets larger, then $(Y - BX)^2$ tends to fluctuate homogeneously throughout the range of X, and

Table 3.—Frequency correlation table showing relationship of 655 plot-sample estimates to associated point-sample estimates of timber in east Texas.

QUANTITY SAMPLED	CLASS LIMITS FOR PLOT ESTIMATES	CLASS LIMITS FOR POINT-SAMPLE ESTIMATES												TOTALS
		SQUARE FEET OF BASAL AREA PER ACRE												
		0-20	20-40	40-60	60-80	80-100	100-120	120-140	140-160	160-180	180-200	200-220	220-240	240-260
		FREQUENCY OF OCCURRENCE												
BASAL AREA	0-20	74	12											86
	20-40	25	72	40	10									147
	40-60	4	32	75	37	11								159
	60-80	2	9	17	52	41	12	4	1					138
	80-100			4	15	23	24	9	1					76
	100-120			1	2	8	5	7	5	1				29
	120-140						1	4	5	2	1			13
	140-160						1		1	1		1	1	5
	160-180													
	180-200										1			1
	200-220													
	220-240												1	
	240-260													1
	Total	105	125	137	116	83	43	24	13	4	1	2	2	655
		GROSS CUBIC FEET PER ACRE												
		0-400	400-800	800-1200	1200-1600	1600-2000	2000-2400	2400-2800	2800-3200	3200-3600	3600-4000	4000-4400		
		FREQUENCY OF OCCURRENCE												
GROSS CUBIC FOOT VOLUME	0-400	223	33	4										260
	400-800	47	104	28	3									182
	800-1200	4	27	45	29	5								110
	1200-1600	1	1	13	21	10	5							51
	1600-2000		2	2	5	7	7	3	2					28
	2000-2400			1	2	3	3	2	1					12
	2400-2800						1	3	2					6
	2800-3200								1	1				2
	3200-3600						1							1
	3600-4000									1	1			2
	4000-4400											1		1
	Total	275	167	93	60	25	17	8	6	2	1	1		655
		GROSS M BOARD FEET PER ACRE												
		0-2	2-4	4-6	6-8	8-10	10-12	12-14	14-16	16-18	18-20	20-22	22-24	24-26	26-28
		FREQUENCY OF OCCURRENCE													
GROSS M BOARD FOOT VOLUME	0-2	266	41	4											311
	2-4	53	73	29	4										159
	4-6	4	17	33	19	7									80
	6-8	1	1	8	17	11	1								39
	8-10	1	1	6	5	7	3	2	1	1					27
	10-12				2	6	3	3		2					16
	12-14					2	2		2	1					8
	14-16							3	3	3					9
	16-18														
	18-20							1			1	1			3
	20-22														
	22-24											1			1
	24-26													1	1
	26-28												1		1
	Total	325	133	80	48	33	9	9	6	7	1	2	1	1	655

Table 4.—Point-sample and plot-sample differences in means and ratios in east Texas, broken down by plot-density class to show behavior of variances about difference of zero and ratio of unity; n degrees of freedom rather than n-1 are employed.

QUANTITY SAMPLED	CLASS LIMITS FOR PLOT ESTIMATES PER ACRE	PLOT FREQUENCY	MEAN DENSITY PER ACRE		DIFFERENCE IN MEAN DENSITY: POINT-PLOT	VARIANCE OF INDIVIDUAL DIFFERENCE ABOUT ZERO	RATIO OF MEANS: POINT / PLOT	UNWEIGHTED VARIANCE OF INDIVIDUAL RATIO ABOUT UNITY
			POINT	PLOT				
BASAL AREA	Sq. Ft.	No.			Sq. Ft.			
	0-20	86	6.5	8.4	-1.9	44	.774	.888
	20-40	147	30.0	30.5	-.5	199	.984	.216
	40-60	159	46.9	49.1	-2.2	308	.955	.129
	60-80	138	70.4	68.8	+1.6	494	1.023	.102
	80-100	76	90.1	87.6	+2.5	489	1.029	.066
	100-120	29	108.3	109.3	-1.0	770	.991	.064
	120-140	13	139.2	132.1	+7.1	469	1.054	.027
	140-160	5	168.0	148.0	+20.0	1,959	1.135	084
	160-180							
	180-200	1	200.0	186.0	+14.0	196	1.075	.006
	200-220							
	220-240							
	240-260	1	230.0	257.0	-27.0	729	.895	.011
	0-260	655	53.8	53.8	0.0	346	.999	.230
GROSS CUBIC-FOOT VOLUME	Cu. Ft.	No.			Cu. Ft.			
	0-400	260	203.3	210.8	-7.5	18,457	.964	.681
	400-800	182	574.8	584.4	-9.6	50,751	.984	.147
	800-1200	110	1,006.3	980.7	+25.6	97,062	1.026	.102
	1200-1600	51	1,423.6	1,381.5	+42.1	154,980	1.030	.081
	1600-2000	28	1,862.9	1,791.0	+71.9	370,202	1.040	.120
	2000-2400	12	1,984.8	2,198.3	-213.5	291,979	.903	.064
	2400-2800	6	2,728.7	2612.7	+116.0	86,405	1.044	.013
	2800-3200	2	3,226.0	3,133.0	+93.0	75,730	1.030	.005
	3200-3600	1	2,173.0	3,440.0	-1267.0	1,605,289	.632	.140
	3600-4000	2	3,699.5	3,724.0	-24.5	36,510	.993	.000
	4000-4400	1	4,177.0	4,178.0	-1.0	1	1.000	.000
	0-4400	655	692.1	691.7	+.4	74,555	1.001	.341
GROSS BOARD-FOOT VOLUME	MBM	No.			Bd. Ft.		MBM	
	0-2	311	814	826	-12	471	.985	.674
	2-4	159	2,841	2,839	+2	1,724	1.001	.215
	4-6	80	5,074	5,047	+27	3,507	1.005	.147
	6-8	39	7,011	6,784	+227	3,714	1.033	.079
	8-10	27	8,341	8,915	-574	11,954	.936	.147
	10-12	16	10,940	10,758	+182	7,798	1.017	.066
	12-14	8	11,435	12,894	-1459	13,718	.887	.084
	14-16	9	15,057	14,950	+107	4,041	1.007	.019
	16-18							
	18-20	3	17,242	19,345	-2,103	22,809	.891	.060
	20-22							
	22-24	1	20,613	22,004	-1,391	1,935	.937	.004
	24-26	1	26,072	25,336	+736	542	1.029	.001
	26-28	1	25,084	27,192	-2,108	4,444	.922	.006
	0-28	655	3,260	3,297	-37	2,313	.989	.404

the best estimate of B is $\frac{\Sigma XY}{\Sigma X^2}$. Table 4 indicates that $(Y - BX)^2$ tends to get larger as X increases, so $\frac{\Sigma XY}{\Sigma X^2}$ would not be a good correction factor.

When $\left(\frac{Y}{X} - B\right)^2$ tends to fluctuate homogeneously throughout the range of X, then $\frac{1}{n} \sum^{n} \frac{Y}{X}$ is the best estimate of B. However, Table 4 indicates that $\left(\frac{Y}{X} - B\right)^2$ tends to get smaller as X increases, so $\frac{1}{n} \sum^{n} \frac{Y}{X}$ would not be a good correction factor.

Between these two situations is the common case where $\left(\frac{Y}{X} - B\right)^2$ tends to get smaller in direct proportion as X increases, or where $(Y - BX)^2$ tends to increase in direct proportion as X increases. The situation in Table 4 seems to be of this sort, and the appropriate B or correction factor would be $\frac{\Sigma Y}{\Sigma X}$, if needed.

Since the ratios $\frac{\Sigma \text{ point estimates}}{\Sigma \text{ plot estimates}}$ for the 655 locations (basal area or volume) were close enough to 1 for the deviation to be attributable to chance, no correction factor was needed here. Had less rigorous calibration or less precise treatment of doubtful trees been employed, however, correction factors derived in this way would have been useful in assessing and correcting bias from either source.

One interesting fact is apparent from Table 4. The only individual class ratio whose deviation from 1 does not appear attributable to chance is in the 0-20 sq. ft. basal area class; the ratio of .774 shown for 86 locations (when taken in conjunction with the .964 cubic-foot ratio and the .985 board-foot ratio in the lowest volume classes) indicates either a slight tendency of the cruisers to avoid thickets of trees smaller than 5 inches in locating plot centers, or else that the high bias in the plot tally caused by 2-inch class grouping of trees smaller than 5 inches was not completely removed even by the improved technique described in the Appendix. Whatever the explanation, basal-area difference in this lowest density class could affect the mean per acre less than ½ of 1 percent.

Additional Analyses

In order to obtain variances needed to estimate the optimum number of points per cluster, point-sampling estimates of basal area per acre were made at both principal and auxiliary points at each location.

The correlation coefficient between the principal and the auxiliary point-sample basal area estimates was +.418, the coefficient of variation for two-point locations was 61 percent, and the mean of the two-point locations was 53.5 square feet per acre.

The analysis of variance for the 655 pairs of points was:

Source of variation	*dfs*	*ss*	*ms*	
Between pairs (location)	654	13,966.1	21.355	
Within pairs (points)	655	5,737.5	8.760	$= V_W$
	1,309	19,703.6	12.595	=
			2	
			6.298	$= V_B$

The expense of point-sampling within locations and between locations (3-mile grid) can be roughly estimated as follows, using approximate car operation costs of $2.00 per moving hour, and 2-man crew costs of $4.25 per hour whether on plot, traveling afoot, or in car.

The cluster expense per location (between clusters) consists of .97 hr. crew-plus-car travel at $6.25 ($6.06), and .46

hr. crew foot-travel at $4.25 ($1.96). Total cost per location, $E_B = \$8.02$. The element expense per point (within clusters) includes .30 hr. crew tally-time and .11 hr. crew foot-travel, totaling .41 hr. of crew time. Thus expense within clusters, $E_W = .41 \cdot \$4.25 = \$1.74$.

These estimates of time do not include normal delays or time lost because of weather, equipment breakdown, leave, etc.

With an estimate of variance between and within locations (V_B and V_W), and cost between and within locations or clusters (E_B and E_W), a cluster-sampling formula can be used to approximate the optimum number of points per cluster for greatest efficiency:

$$\text{Points per cluster} = \sqrt{\frac{V_W}{V_B} \cdot \frac{E_B}{E_W}} = \sqrt{\frac{8.760}{6.298} \cdot \frac{8.02}{1.74}}$$

$$= 1.18\sqrt{4.61}$$

$$= (1.18)(2.15)$$

$$= 2.54 \text{ points per location or cluster}$$

Thus, if the present system of a 3-mile grid were to be continued using point-sampling, and if the above costs and variances were valid, it would be slightly more efficient to take 3 points per location instead of the 2 actually taken.

One of the important advantages of the point-sample method is that it permits one man to work alone efficiently. Compared with a two-man crew, one man will need somewhat more tally time at a point, but the cost of travel per location is greatly reduced. Using the above car operation cost and a 1-man crew cost of $2.25 per hour, and estimating that a 1-man crew will require 10 percent more travel time by car and foot and .50 hour tally time at each point, cluster expense would be $5.67 per location and element expense $1.39. For 2-point locations the 1-man crew cost would total $8.45 vs. the 2-man crew cost of $11.50, a reduction in cost of 26 percent per location.

Because of difficulty of terrain and safety hazards it is not always practical for one man to work alone. To the extent that conditions permit, however, use of one-man crews offers the opportunity to reduce cost substantially.

Obviously other modifications would further change the picture. A different grid-spacing, a different size of angle-gauge, the use of 1-man instead of 2-man crews, and possibly the use of helicopters instead of cars would modify the optimum number of points per cluster. It is also possible that the ratio of variance within cluster to that between clusters might be slightly different for volume than for basal area.

Conclusions

This exploratory study demonstrated how comparisons between point-sampling and plot-sampling estimates should be analyzed. Point-sampling estimates of basal area and volume per acre were found to be unbiased with respect to plot-sampling estimates when precautions were observed Local cost information was not secured fo. ¼-acre plot-sampling, so relative efficiencies cannot be estimated, although certain advantages of point-sampling were quite obvious (possibility of 1-man crews, growth and error calculations). Coefficients of correlation and variation in southeast Texas may not be valid for other areas, but they are at least indicative of the comparative magnitudes and trends apt to be exhibited elsewhere, and may be useful in sampling design. A rough estimate of optimum cluster-size indicated that 3 points per cluster would have been slightly better than 2, but this conclusion might be modified if crew, grid, gauge, or conveyance is changed. Finally, a technique was developed for reducing bias in basal-area estimates when tree frequency only has been tallied by rather broad d.b.h. classes (2 inches or more).

Appendix

Although the point-sample included all qualified trees larger than 1 inch in d.b.h., the plot-sample excluded trees less than 5

inches in d.b.h. from the ¼-acre plot tally. Frequency of trees whose d.b.h. was 1 to 3 inches and 3 to 5 inches was sampled only on a concentric 1/40-acre plot, and diameter was recorded by two-inch classes rather than the tenth-inch classes used for trees larger than 5 inches. To permit more accurate calculation of the basal area per acre for 1- to 5-inch trees on the plot-sample, a new technique was worked out which recognized the effect of J-shaped small-tree frequency distributions on mean tree basal area. This new method is described below, since it is much less biased than the commonly used method which assumes that all trees are clustered at the nominal midpoint of the broad diameter class.

A convenient J-shaped distribution commonly encountered in forests is that popularly known as de Liocourt's (with integrals in geometric progression, so that on semilog paper the logarithmic frequency ordinate plots as a straight line over the arithmetic abscissa, which is diameter). The generating function of the distribution is $y = ke^{-\frac{x}{a}}$, where (y) is a frequency ordinate and (x) is diameter; (a) and (k) are parameters which can be empirically deduced from actual stand table data, although (k) is never explicitly needed.

The frequency per acre (f) of trees in the diameter interval (d) to (d + m) is:

$$f = \int_{d}^{d+m} Ydx = ake^{-\frac{d}{a}}\left(1 - e^{-\frac{m}{a}}\right),$$

when (m) denotes a constant width of diameter class; the ratio of frequencies in two adjacent diameter classes is:

$$\frac{f}{f'} = \frac{\int_{d}^{d+m} Ydx}{\int_{d+m}^{d+2m} Ydx} = e^{\frac{m}{a}}$$

From the above identities, it is apparent that: $a = \dfrac{m}{2.3026 \log_{10}\left(\frac{f}{f'}\right)}$. Calculation of (k) is not necessary. Mean basal area per tree in an interval (d) to (d + m) can be calculated when $\frac{f}{f'}$ (a), (d), and (m) are known.

$$\text{It is} \frac{.00545415 \int_{d}^{d+m} X^2 Ydx}{\int_{d}^{d+m} Ydx}$$

which can be evaluated as follows:

$$.00545415\left[(d+a)^2 + a^2 - \frac{2m(d+a) + m^2}{\frac{f}{f'} - 1}\right]$$

TABLE 5. Comparison of mid-class and mean-tree methods of computing basal area in 2-inch and in 4-inch diameter classes on plots in east Texas.

Class limits	Number of trees per acre	Mid-class method: Mid-class tree d.b.h.	Mid-class method: BA of mid-class tree	Mean-tree method: Mean tree d.b.h.	Mean-tree method: BA of mean tree	Basal area per acre: Mid-class method: Two 2″ classes	Basal area per acre: Mid-class method: Single 4″ class	Basal area per acre: Mean-tree method: Two 2″ classes	Basal area per acre: Mean-tree method: Single 4″ class
Inches		*Inches*	*Sq. ft.*	*Inches*	*Sq. ft.*	*Sq. ft.*	*Sq. ft.*	*Sq. ft.*	*Sq. ft.*
1–3	224.3	2	.0218	1.90	.0197	4.89	.....	4.42	.....
3–5	73.7	4	.0873	3.86	.0812	6.43	.....	5.98	.....
1–5	298.0	3	.0491	2.53	.0349	11.32	(14.63)	10.40	(10.40)

Multiplying this by (f) for the class in question will, of course, give total basal area in the desired diameter interval.

The 1/40-acre plot-samples on each ¼-acre plot indicated that there were 224.2553 trees per acre between 1 and 3 inches in diameter (called two-inch trees), and 73.6778 trees per acre between 3 and 5 inches in diameter (called four-inch trees). Thus $\frac{f}{f'} = 3.04373$ where diameter interval (m) = 2 inches. Fitting the distribution previously discussed indicated that (a) = 3.22856. The basal area of the mean tree in the class interval 1 to 3 inches was .0197 square feet (a tree with d.b.h. = 1.90 inches), and in the class interval 3 to 5 inches was .0812 square feet (a tree with d.b.h. = 3.86 inches). The basal area of the mean tree for the 2 classes combined (i.e., the interval 1 to 5 inches) was .0349 square feet (a tree with d.b.h. = 2.53 inches).

The tabular comparison in table 5 indicates that use of mid-class tree basal area for each 2-inch class would have resulted in a high bias of 8½ percent (about 1 square foot per acre). If the tree at the nominal midpoint (3 inches) of a single 4-inch class (1–5 inches) had been used, the high bias would have been more than 40 per cent (over 4 square feet per acre).

Even the 1 square foot basal area bias shown above for mid-class trees of each 2-inch class would have vitiated comparability of plot-sample means with point-sample means, but the mean-tree method described above made use of observed $\frac{f}{f'}$ to take into account the J-shape of the frequency curve and minimize the bias.

Errata

In *Suggested modifications of the standard Douglas-fir site curves for certain soils in southwestern Washington* by Willard H. Carmean (FOREST SCIENCE 2: 242-250), an error occurred in the legend of figure 1 (page 244). The symbols for "Sands" and for "British Columbia Forest Service" should be interchanged in this figure.

In *Measurement of acorn crops* by Leslie W. Gysel (FOREST SCIENCE 2: 305-313), a line was omitted on page 308. The sentence beginning with the fifth line in the first column should read: "Dalke (1953) describes a study of mast yields *based on weekly collections of seed in mil*-acre plots established at one-chain intervals along 5.6 miles of surveyed lines." The italicized words were those omitted.

Infection Courts of Butt-rotting Fungi in Balsam Fir

BY
D. R. REDMOND

BALSAM FIR, *Abies balsamea* (L.) Mill., is very commonly defective because of decay (Spaulding and Hansbrough, 1944). A considerable amount of this defect occurs as butt rot, Basham *et al.* (1953) having reported cull from this source in 54 percent of the 2799 mature trees studied. They found butt rot to reach occasionally to a height of 20 ft., but the average was between 4 and 5 ft.

It is commonly stated that a high percentage of butt rot infections originate in the roots. Zon (1914) considered that tap roots, if formed, died and rotted away, often becoming entrance points for fungi causing butt rots. McCallum (1928) found white feather rot in the bole of balsam fir to have originated through the roots in 95 percent of the trees containing it. Davidson (1955), having found butt rot in 55 percent of the trees between 61 and 120 years of age, stated that in the majority of cases the fungi responsible gained entrance through roots. Spaulding and Hansbrough (1944) found that butt decay occurred in over 50 percent of the trees by the time they reach 65 years of age and traced the origin of 89 percent of these infections to the roots. Kaufert (1935), in examining root systems of young balsam fir, located some small broken and dead roots in almost every tree more than 30 years of age. He considered these to have resulted probably from frost heaving or strain caused by the trees bending in the wind. Also, he thought broken roots were probably the entrance points for the fungi, since several were found with incipient decay near the broken tips. White (1951) examined 20 young balsam fir seedlings chosen at random on an acre plot in Ontario. Rootlets and basal parts of all 20 were badly decayed, but the type of wounds leading to infections was not determined.

The literature indicates that 85 to 95 percent of the butt rot infections in balsam fir arise in the roots, the remainder arising from scars near the root collar, but very little information is recorded on the types of entrance courts responsible for these infections.

Observations and Results

During 1955 a study was begun in northern New Brunswick to determine the effect of repeated heavy defoliation by the spruce budworm, *Choristoneura fumiferana* (Clem.), on the rootlet conditions in balsam fir. The root systems of 18 trees between 65 and 125 years old, at stump height, were completely excavated. These trees were defoliated first in 1950 and the proportion of new foliage removed that year and during each of the succeeding four years was 50, 80, 100, 100, and 100 per-

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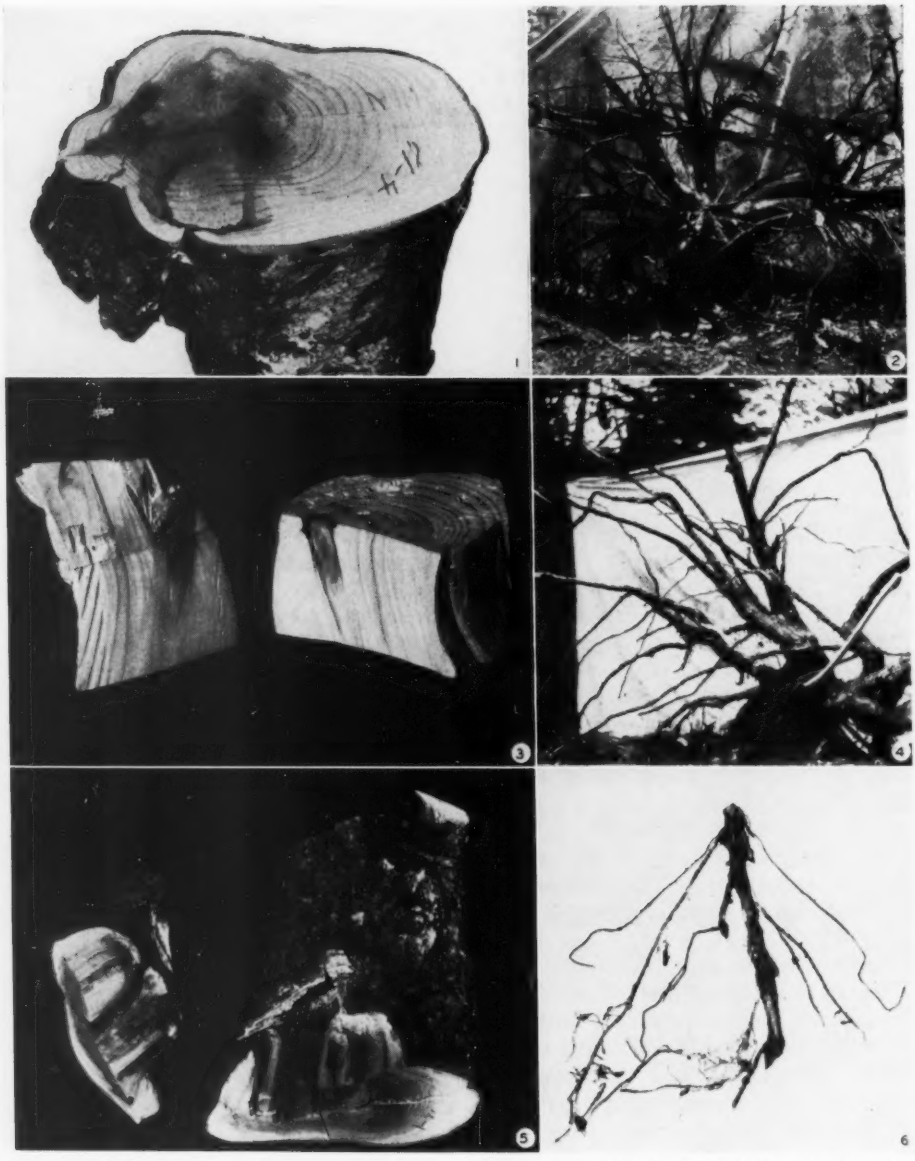

FIGURE 1. *Cross section through a balsam fir root showing one healed wound (lower left) and a second (lower right) in the process of being healed. Decay has originated at each. Decay in the center originated at a third wound not shown.* FIGURE 2. *Root system of a mature balsam fir tree showing profuse and abnormal branching of several primary roots.* FIGURE 3. *Longitudinal section through a primary root of balsam fir, showing an embedded dead root, having 12 annual rings, that died 35 years ago.* FIGURE 4. *Root system of a balsam fir tree illustrating normal development. Primary roots taper uniformly and secondary roots originate at intervals.* FIGURE 5. *A balsam fir root split through a crotch that has strangled another root. Note rotten strangled root and decay that has entered living root at this point.* FIGURE 6. *Balsam fir root showing several elongate, rarely branched rootlets originating just behind a dead tip.*

TABLE 1. Number of annual rings in primary roots near foci and at bases of secondary roots in one balsam fir tree, 1955.

Focus No.	No. of annual rings								Period during which focus arose
	Primary root	No. of secondary roots							
		1	2	3	4	5	6	7	
1	48	39	37	35	31	29	29	24	1907–1916
2	48	37	35	35	34	33	31		1907–1918
3	46	36	36						1909–1919
4	45	36	36	34	34				1910–1919
5	45	38	33	33					1910–1916
6	43	32	30	25					1912–1923
7	59	49	30						1896–1906
8	58	53	46	42	36	35			1897–1902
9	(a)	(a)	34						Before 1921

(a) Count impossible because of decay.

cent.[1] In 1955 the budworm population was low in the study area and production of new shoots that escaped attack amounted to about 20 percent of what would have been produced by trees of this size under normal conditions. Therefore, foliage conditions were considered to indicate a stage of initial recovery.

These trees were found to have suffered mortality of 85 to 90 percent of their rootlets by early September, 1955, whereas less than 10 percent of the rootlets were dead in trees that had suffered no defoliation from budworm. Also, in defoliated trees, many roots 2 to 4 millimeters in diameter were dead. Evidence of initial improvement in root conditions was found frequently in the form of prolific branching at the living end of small roots with dead tips. Figure 6 shows several new rootlets up to 10 or more centimeters long originating near the interface between living and dead tissue. These rootlets differed conspicuously from new rootlets on healthy trees, not only because of their excessive length, but also in the small number of mycorrhiza, short roots, and branches produced. It is assumed that these long rootlets are basic to formation of a pattern of branching observed in the large roots of some trees where the primary roots often ceased to extend radially at a point 2 to 4 or 5 ft. from the root collar. At this point there was a focus of profuse branching from which the secondary roots radiated. A root system with several of these foci is shown in Fig. 2. The manner of branching of balsam fir roots under normal conditions is illustrated by Fig. 4, which shows the roots tapering at a steady rate as they radiate from the base of the stem.

Examination of deformed primary roots at the focus of branching frequently revealed buried remnants of dead roots (Fig. 3). Decay often obliterated conditions but dead roots often were observed to contain up to 10 or 12 annual rings. Also, considerable evidence was accumulated to indicate that many of these foci arose because of injury resulting from the severe budworm attack between 1914 and 1920. A count of the annual rings present in the primary root near the focus and in each secondary root near its base permitted dating the approximate time of the origin of the deformity. Table 1 shows the ages of roots from 9 foci in the root system of one tree. Foci numbers 1 to 6, as listed in the table, can be considered to have arisen at

[1]Information supplied through the courtesy of Mr. D. G. Mott, Forest Biology Laboratory, Fredricton, N. B.

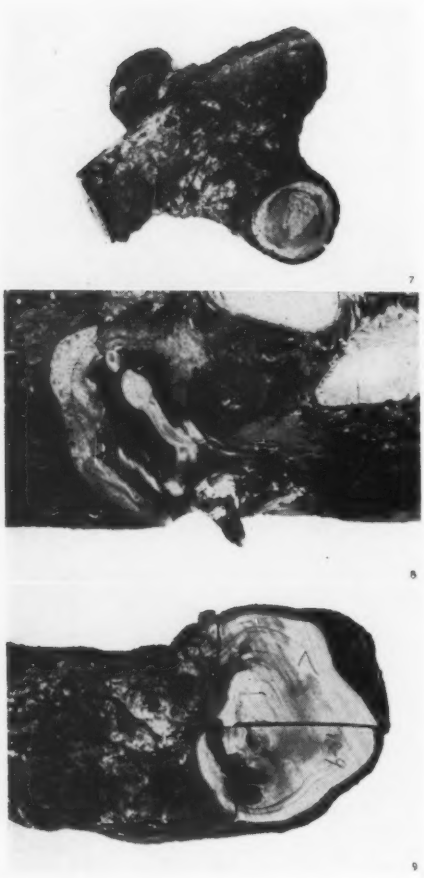

FIGURE 7. *Graft between two living balsam fir roots. Note decay.*

FIGURE 8. *Balsam fir root showing dead side root, bottom, from which a lesion originated on the large root and through which decay has entered.*

FIGURE 9. *Wound on lower surface of a balsam fir root that has admitted decay. Note in several growth rings layers of traumatic cells that suggest periodic wounding by stones.*

the time of the previous budworm outbreak in a manner similar to that illustrated by Fig. 6.

The direction of development of the secondary roots also indicated that they arose at a time when there was little, if any, competition from other rootlets in the soil. In Fig. 2 roots are seen to radiate from foci toward the base of the tree, a soil area that would be unattainable because of root competition under a tree with a healthy root system. Roots could develop freely in this manner only during a period of recovery from severe rootlet mortality such as was found in badly defoliated trees in 1955 or as described by Swaine *et al.* (1924). They reported all rootlets below two millimeters in diameter dead and completely rotted on many trees examined six months prior to their death from budworm attack.

Eleven (61 percent) of the trees examined in this study contained decay that had entered through roots and extended above stump height. All contained decay in one or more of the primary roots. A thorough examination was made of all deformities in primary roots in these trees to determine their number that could have arisen as a result of the budworm outbreak between 1914 and 1920 as well as the relative importance of buried dead roots in providing courts of infection for wood-destroying fungi causing butt rot. This revealed that the time of origin of only 23 percent of these deformities could be attributed to a disturbance occurring around 1914 to 1920 and dead roots could be found in only 30 percent of these. Dead roots were found in 19 percent of the deformities that could not be dated to a period of insect attack.

Evidence of wounding (Fig. 9) could be seen on the surfaces of some specimens but many healed-over wounds were uncovered when the specimens were sectioned or split. Fig. 1 shows a root with two wounds from which decay has originated, one healed over in typical fashion, the other in the process of being healed. Wounds occurred frequently in crotches or at the base of sec-

TABLE 2. Source of decay in 105 infected roots contained in 148 samples of primary roots of balsam fir.

Type of infection court	No. occurring	Occurrence of infections		
		Number infected	Percentage of types of court	Percentage of all infections
Wounds in crotches	67	49	73.1	35.0
Surface wounds	89	52	58.7	37.1
Buried dead roots:				
Originating between 1914–1920	10	4	40.0	2.9
Originating at other times	22	14	63.6	10.0
Unknown	21	21	100.0	15.0
	209	140	67.0	100.0

ondary roots and decay was found often to originate there. These wounds often formed around stones completely embedded in the growing roots. In some cases a root from another tree was strangled and killed in a crotch (Fig. 5). Inoculum to infect the living root was provided by the decay of the killed root. Also, death of a secondary root may result in a lesion on the primary root (Fig. 8). Lesions associated with crotches were found in 40.5 percent of the specimens.

Wounds not associated with crotches were found in 49 percent of the samples. Nearly always these occurred on the under side of roots, presumably because of stone bruises. A layer of traumatic cells that extended tangentially and longitudinally was found associated with all wounds (Fig. 9). It was considered that the position of this layer in the growth ring indicated the season during which wounding occurred. Of 78 wounds examined, traumatic cells composed the first layers of early wood in 69 percent of the cases. They were found in the center of the ring or in the late wood in 18 percent of the samples, and their position could not be determined for 13 percent of the wounds. This evidence indicates a large percentage of these wounds to have originated during the dormant season. It is considered that they may have arisen through contact with stones in one or more of the following ways: friction during swaying in the wind, upward thrust of stones by frost heaving, increased diameter of the roots causing contact with stones, and increased weight of the tree resulting in downward thrust onto stones.

Grafts between roots (Fig. 7) were found occasionally and decay always was present. These were usually but not always between roots of the same tree.

Although only the deformed portions of primary roots were collected for sectioning, decay was found in 105 of the 148 specimens examined from 18 trees. No doubt it would have been found in more of them if the entire roots had been examined. Table 2 contains data showing that surface wounds in crotches account for a high percentage of the entrance courts for root-rotting fungi. Although buried dead roots provide entrance points for about 13 per cent of the infections it is very revealing to note that those originating during the previous period of budworm defoliation accounted for only about 3 percent. However, many of the crotch wounds studied did occur in the foci resulting from root recovery.

Isolations made from decayed portions of roots yielded the following fungi in culture: *Armillaria mellea* (Vahl ex Fr.) Quél., *Coniophora puteana* (Schum. ex Fr.) Karst., *Corticium galactinum* (Fr.)

Burt, *Polyporus balsameus* Pk., *Stereum sanguinolentum* Alb. and Schw. ex Fr. No correlation could be found in this small sample between the type of wound and the species of fungus present. It is doubtful if one exists because both brown and white rots were found to have originated from each type of wound. Also, both types of rot occurred adjacently in many specimens.

Swaine *et al.* (1924) found *Armillarea mellea* to be very prevalent in roots of trees severely defoliated by budworm, practically every tree having been attacked at the time it was dead or shortly thereafter. The fungus was reported to have gained entrance at the tips of dead rootlets and to work rapidly up the roots to the butt of dying trees. No dead trees were examined in the present study and no recent infection by *A. mellea* were observed. However, rhizomorphs of this fungus were found invading the outer dead bark of all subterranean portions of structural roots. There was no evidence of attack through living bark.

Discussion and Summary

Stillwell (1956), studying trees that had suffered considerable top-killing as a result of the budworm outbreak between 1914 and 1920, found this damage to be evident in 1955 in the form of forking, marked crooks, or sweeps in the bole. Often the remnants of dead leaders were buried and if they contained 5 or more annual rings or were greater than 0.5 inch in diameter at the point of death they invariably served as entrance points for top rot. Although no data were given on the general frequency with which decay from this cause may be expected, he found about 10 percent of the trees in some small plots thus infected.

In comparing the two types of damage resulting from severe defoliation by the spruce budworm, it would appear that dead roots are of less significance than dead tops in providing courts of entry for decay. Although dead roots provided means of entry for 13 percent of all infections found in roots, only about 3 percent arose from dead root tips resulting from budworm defoliation. Decay originated most commonly in wounds in crotches or from stone bruises and in no trees was the presence of decay related entirely to dead roots caused by budworm defoliation.

Data presented here confirm previous reports that the incidence of butt decay in living balsam fir trees is very high, especially after they have attained an age of 65 years. Besides causing a high volume of cull in living trees, butt rots through weakening roots and butts contribute greatly to a large amount of windfall. Mortality from wind throw is often very high in balsam fir stands over 75 years of age.

Since it would be impossible to protect roots of balsam fir from being wounded where they contact stones, a significant reduction in the incidence of butt rots and undue loss in volume can be obtained only through adoption of the shortest rotation that will produce trees of merchantable size.

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A Ratchet Wrench for Over-size Increment Borers

Equipment Note by John W. Duffield, Technical Director
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The increment borers generally used for determining age and radial increment have bits which cut cores up to 4.5 millimeters in diameter. These bits, especially when deeply embedded in a tree, offer considerable resistance to turning, with the result that the collection of a large series of cores becomes rather strenuous work. For the collection of cores which can be used for study of wood properties such as specific gravity or tracheid length, bits which cut cores up to 8 or 11 millimeters in diameter are available on special order. These over-size bits are extremely difficult to drive with the usual cross handle, particularly in trees with heavy or hard wood. Part of the difficulty in driving an increment borer results from the fact that the operator must apply torque with the handle in all positions from horizontal to vertical. Not all of these positions are equally advantageous to the operator.

The mechanic's ratchet wrench offers a solution to this difficulty by enabling the operator to apply torque through the arc which he finds most convenient. Figure 1 shows such a wrench modified for driving a 12 inch by 8 millimeter increment borer bit. The wrench differs from the commonly-used socket wrench handle in that the driving socket extends through the handle, thus making it possible to use the aligning spindle and core extractor without removing the driving handle. The wrench handle, which can be secured from any of the larger tool supply houses, should be modified by having a length of pipe brazed to provide an arm opposite the original handle. This avoids putting an unbalanced strain on the bit. A further modification is necessary in order to fit the driving head to the square butt of the bit. Finally, a retaining lock, similar to that provided on the regular increment borer handle, should be added to facilitate retraction of the bit. In the wrench handle illustrated, a knurled knob at the end of the handle is used to reverse the ratchet for retraction.

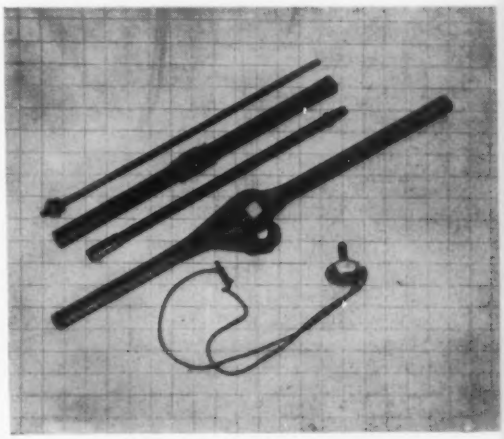

FIGURE 1. *Twelve-inch, 8 millimeter increment borer as supplied by manufacturer plus modified ratchet wrench handle and aligning spindle.*

Also illustrated in Figure 1 is a knob fitted with a spindle which fits the inside of the rear end of the bit. This device, suggested by Reineke,[1] enables the operator to start the bit into the tree with a minimum of wobble and results in straighter cores than are usually obtained by free-hand operation.

[1]Reineke, L. H. 1941. A new increment core instrument and coring wrinkles. J. For. 39: 304-309.

Classification of the Spatial Distribution of Trees Using the Area Sampling Method

BY
CHERNG-JIANN SHIUE
RONALD BEAZLEY

THE QUADRAT METHOD is a standard sampling technique used in ecological studies, and in the case of forests, the trees are usually sampled by quadrats which are 10 meters on edge with an area of approximately 1/40 acre. Three values are commonly used as standard measures to show the relative abundance and importance of any species in the forest (Curtis, 1951). These are: (1) density: the average number of trees of each species per acre, (2) dominance: the average basal area of each species per acre, and (3) frequency: the probability of each species being present on any quadrat. Density and dominance do not yield information about the spatial distribution of trees and the frequency shows only the ratio between the occupied and non-occupied quadrats.

Recognizing the importance of relative clumpiness or evenness as well as the variation of tree spacing within clumps, it appears desirable to develop additional qualitative and quantitative measures which will indicate these spatial relationships consistently. Ker (1954) suggested methods of fitting particular curves such as the Poisson or the negative binomial to frequency distributions of loblolly pine seedlings. The method proposed here is not comparable because it avoids fitting particular curves, yet it provides a rational method of classifying many possible spatial relationships, assuming no stratification of tree distributions in the populations being considered.

Classifying Relative Spatial Tree Distributions

The problem at hand, which is well known to most foresters and other natural scientists, is that of describing the spatial relationships involved in a plant community, whether on the basis of stems, diameter classes, basal area classes or any other meaurable quality pertaining to individual trees or other plants as they appear in groups.

The first thought which comes to mind is that of describing the areal grouping by gridding the whole population into areas of equal size and recording the population frequency of these areas according to numbers of trees per area, diameter classes or basal area classes and then attempting to fit a curve to the frequencies so found. But measuring a whole population is usually out of the question due to cost, and furthermore fitting one of an infinite number of possible curves is time consuming and in fact, unnecessarily refined for use in prac-

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tice. To sample the population and then to fit a curve to the sample frequency creates a still more difficult situation because one is then faced with the presently impossible problem of making a probability statement as to whether the curve of the sample frequency distribution actually is the *same* as the unknown parent population frequency distribution. It follows then, that the problem has the three objectives of determining a method which, (1) avoids curve-fitting and unnecessary refinement of results, i.e., provides a method of classifying spatial frequency distributions rather than mathematically formulating each, (2) is amenable to sampling procedure and (3) provides for objective probability statements concerning the classifications. The remainder of this paper shows how these objectives may be satisfied. It will be seen also that the general method may be applied to the classification of sample frequency distributions other than those involving spatial relationships, but for the sake of brevity these will be ignored.

Trees of a given species may assume various spatial associations, one with the other, in a particular forest. If the plant community is divided into quadrats, the frequency distribution of trees occurring on these quadrats consistently describes the relative tree association of this population in terms of clumpiness and variation of tree spacing within clumps. In this discussion a spatial tree distribution will be considered to exist only with relation to some particular areal designation such as the 1/40 acre plot, because the frequency distribution itself will change at some point as the plot size is changed.

In any forest community, if the plot size is made large enough, the relative distribution will tend to be even (non-clumpy); if the plot size is small enough the plots will show only the presence or absence of trees in the ratio of the total basal area to the total non-occupied forest land—in this case any measure of clumpiness or evenness disappears.

Between these extremes any reasonable standard plot size may be adopted according to the general size class of the trees being studied, and the biological relationships of interest. For example, 1/40-acre plots may be used in sampling trees larger than 3 in. in diameter, 1/250-acre plots for saplings from 6 ft. high to 3 in. in diameter and mil-acre plots for seedlings (less than 6 ft. high). The method to be described may be used with any size of plot, recognizing, of course, that a change in plot size may change the type of population distribution described.

Major Types of Distributions

Figure 1 indicates nine major types of population frequency distributions which may occur in relation to the quadrats into which a hypothetical forest has been divided. Since the quadrats are of constant size in each case, the differences among the frequency distributions are due to differences in the spatial association of stems on the ground in each plant community. In each example the total number of plots (N) in the assumed, oversimplified population is 25 and the average number of trees per plot (μ) is 2.

Diagram A in the center of Figure 1 indicates a rectangular distribution in which the frequency of occurence of plots containing 0, 1, 2, 3, or 4 trees is the same. This may be an unlikely distribution to expect biologically, but it provides a useful standard from which to describe the other kinds of distributions. The remaining eight types shown may be described in terms of differences in *central tendency* and *skewness* from the standard or rectangular distribution. Central tendency is defined as the degree of concentration of frequencies over the mean class. It is positive or negative when the frequency over the mean class is greater or less than, respectively, the expected frequency for the same class in a rectangular distribution. Skewness is defined as departure from symmetry, where symmetry in turn is defined as being the case where the frequencies on either side of the mean value are equal.

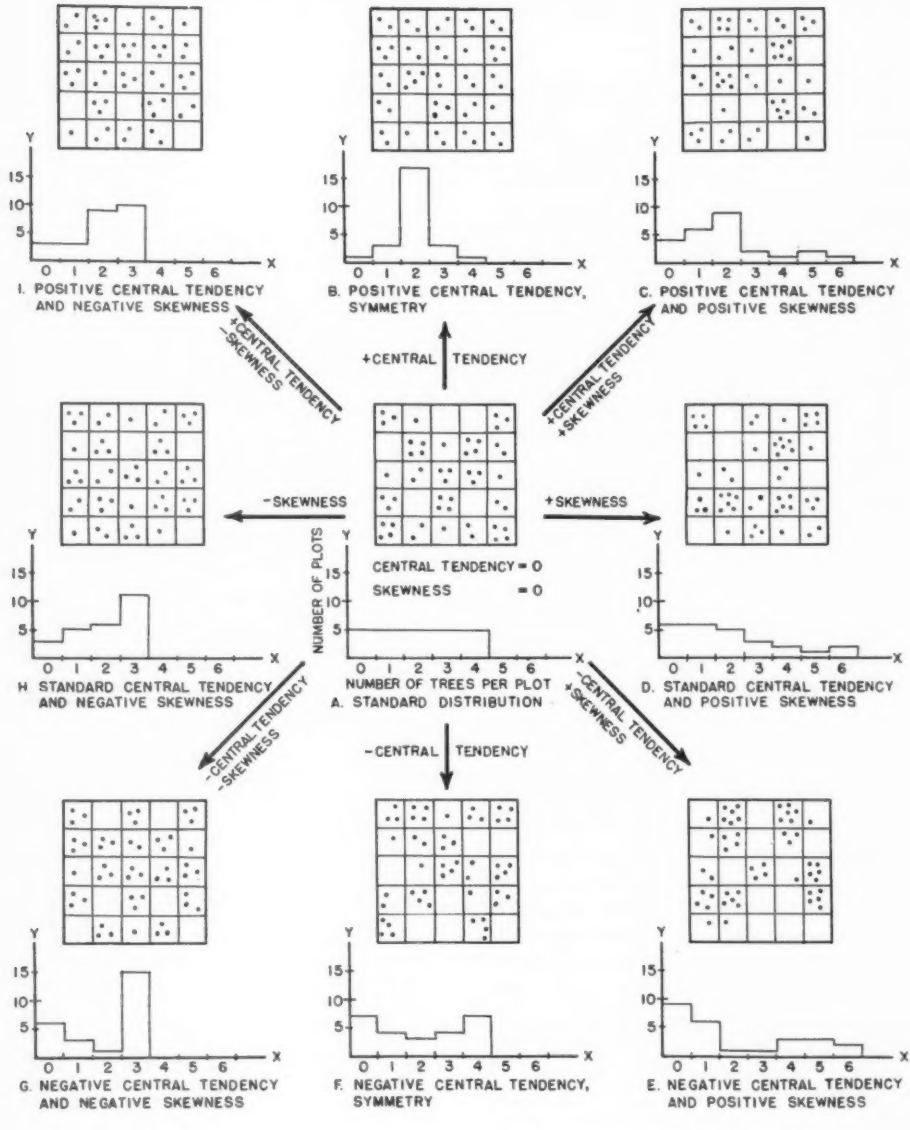
I. POSITIVE CENTRAL TENDENCY AND NEGATIVE SKEWNESS
B. POSITIVE CENTRAL TENDENCY, SYMMETRY
C. POSITIVE CENTRAL TENDENCY AND POSITIVE SKEWNESS
+CENTRAL TENDENCY -SKEWNESS
+CENTRAL TENDENCY
+CENTRAL TENDENCY +SKEWNESS
-SKEWNESS
+SKEWNESS
NUMBER OF PLOTS
CENTRAL TENDENCY = 0
SKEWNESS = 0
NUMBER OF TREES PER PLOT
A. STANDARD DISTRIBUTION
H. STANDARD CENTRAL TENDENCY AND NEGATIVE SKEWNESS
D. STANDARD CENTRAL TENDENCY AND POSITIVE SKEWNESS
-CENTRAL TENDENCY -SKEWNESS
-CENTRAL TENDENCY
-CENTRAL TENDENCY +SKEWNESS
G. NEGATIVE CENTRAL TENDENCY AND NEGATIVE SKEWNESS
F. NEGATIVE CENTRAL TENDENCY, SYMMETRY
E. NEGATIVE CENTRAL TENDENCY AND POSITIVE SKEWNESS

FIGURE 1. *Major tree distribution types as illustrated by hypothetical populations.*

In Fig. 1-B, the trees are almost evenly distributed on the ground, which is indicated by positive central tendency and lack of skewness, while Fig. 1-F has an aggregative or clumpy distribution on the ground indicated by negative central tendency and lack of skewness. D and H show variations from the standard distribution due to positive or negative skewness. On the other hand, I and C, and G and E show the effects of skewness on positive and negative central distributions, respectively.

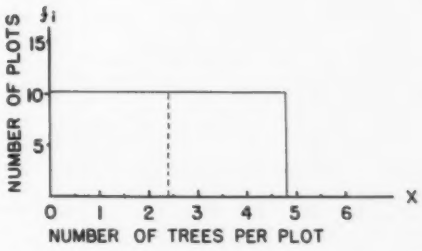

FIGURE 2. *Frequency distribution of the standard or rectangular form.*

Distribution Classifying Tests

Two tests are suggested to infer which distribution best describes a given forest population, on the basis of random sampling from that population (although random-start systemmatic samples may be practicable in practice). The tests are described below with an example using the same set of hypothetical sample data throughout. These data are:

No. of trees per plot (x_i)	0	1	2	3	4	5	6	Total
No. of plots (frequency, f_i)	88	36	8	8	16	24	20	200
Relative frequency $f(x) = \frac{f_i}{\Sigma f_i}$	0.44	0.18	0.04	0.04	0.08	0.12	0.10	1.00

Total number of trees $= \Sigma x_i f_i = 380$

Average number of trees per plot $= \bar{x} = \frac{\Sigma x_i f_i}{\Sigma f_i} = \frac{380}{200} = 1.9$

It is important to note that in tests involving central tendency, the frequencies (f_i) of the mean class ($\bar{x}$) and the one following it ($\bar{x} + 1$) should exceed 5, because these tests are based on the transformation of the binomial distribution so that it approaches the normal where $f_i > 5$. In the data above, $\bar{x} = 1.9$, therefore the number of plots in each of the tree classes (x_i) 1 and 2 should exceed 5.

Skewness Test

This test is designed to find out if the frequency is distributed equally on either side of $\bar{x} + \frac{1}{2}$, which is in this case $1.9 + 0.5 = 2.4$. In a rectangular distribution, as in Fig. 2, the cumulative frequencies on either side of the dashed line ($\bar{x} + \frac{1}{2}$) are equal, i.e. there is no skewness, hence the hypothesis is made that there is no difference in cumulative probability on either side of $\bar{x} + \frac{1}{2}$.

From the given sample data, the cumulative probability from 0 to 2.4 is:

$$\sum_{x_i=0}^{2.4} f(x_i) = 0.44 + 0.18 + 0.04 \times 0.4 = 0.636,$$

while the expected value for a rectangular distribution is 0.500. Hence the departure due to skewness (d_s) $= 0.636 - 0.500 = 0.136$. The significance of this departure may be tested by using Table 1 which shows the expected values of departures from a rectangularly distributed population

TABLE 1. Departures[1] from the expected probability value[2] of a rectangular distribution due to skewness at P = 0.05 and P = 0.25.

Sample Size	P = 0.05	P = 0.25
25	.171	.068
30	.155	.062
35	.143	.058
40	.133	.054
45	.125	.051
50	.119	.048
60	.108	.044
70	.100	.041
80	.093	.038
90	.087	.036
100	.083	.034
125	.074	.030
150	.068	.028
200	.058	.024
300	.048	.019
400	.041	.017
500	.037	.015

[1]Tabular departure $= \frac{t}{2}\sqrt{\frac{1}{n}}$,

where the t value is obtained from the table of cumulative "student's" distribution (Mood, 1950).

[2] Expected value = 0.50.

of plot frequencies due to sampling variation at the 0.05 and 0.25 probability levels, where the expected cumulative frequency value = 0.500.

Since in this instance n = 200, the tabular value of d_s at P = 0.05 is 0.058 and of d_s at P = 0.25 is 0.024. The observed value of d_s is 0.136, hence the probability of obtaining a value as large as this due to sampling variation is less than 5% and is termed *significant skewness*. The skewness is positive or negative in accordance with the sign of the observed d_s, in this case positive.

In addition to the instance of significant skewness two other cases of skewness are recognized, viz., *predominant skewness* when $0.05 < P < 0.25$, being either positive or negative, and *symmetry* predominant when $P > 0.25$, i.e., a tendency to zero skewness. Assuming the mean and central tendency to be constant, positive skewness indicates that few plots tend to have a large number of trees per plot compared with the mean and that most have few or zero trees per plot, which in turn indicates great variability of spacing of trees. Negative skewness correspondingly indicates a tendency to small variability of spacing of trees.

Having described one of the two qualities of the distribution causing it to differ from the rectangular distribution, the next test permits the drawing of conclusions about the remaining quality, central tendency.

Central tendency test

Briefly, this test is designed to find out if the value of the frequency over the mean class is different from that of a rectangular distribution, and if so, to what degree of probability. Central tendency indicates the occurrence of openings or thinly distributed trees in forest communities which are otherwise evenly spaced; while skewness tends to indicate relative variation of spacing of trees.

Let: $p_o = 0.04 \times 0.1 + 0.04 \times 0.9 = 0.04$, the observed relative frequency of the mean class, $\bar{x}$ to $\bar{x} + 1$, i.e., 1.9 to 2.9.

$p_E = \frac{1}{2\bar{x} + 1} = \frac{1}{4.8} = 0.208$, the expected value for the relative frequency at the same class, $\bar{x}$ to $\bar{x} + 1$ of a rectangular distribution.

Then, the departure due to central tendency $= d_c = p_o - p_E = 0.040 - 0.208 = -0.168$.

From Fig. 3, where n = 200, $\bar{x} = 1.9$, and P = .05, the tabular departure of $d_c = -.048$. Since the value of the observed d_c is greater than the tabular d_c, ignoring sign, the distribution is said to have *significant central tendency*, which is different from the standard (rectangular) form, and the departure is negative, thus the dispersion of tree stems on the ground is clumpy relative to the plot size used. In addition to significant central tendency two other cases

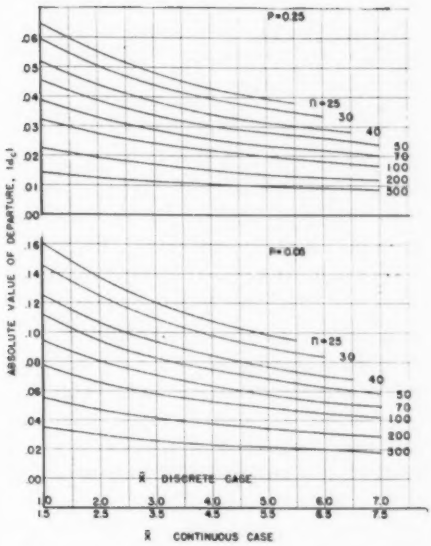

FIGURE 3. *Expected departure of central tendency (d_e) for sample sizes of 25 to 500 at $P = 0.05$ and $P = 0.25$.*

of central tendency are recognized, viz., *predominant central tendency* when $0.05 < P < 0.25$, being either positive or negative, and *standard central tendency* when $P > 0.25$.

To aid in classifying the various combinations of skewness and central tendency according to the *probability* of their occurrence, a key is provided as shown in Fig. 4 describing in total, 25 types. Using the key this distribution is classified as type No. 20, having a significant negative central tendency with positive skewness significant.

If the number of trees per plot has a wide range with $\bar{x} > 7$ a class grouping is necessary. The class values may be assigned as 1, 2, 3, 4 . . . . so that $\bar{x} < 7.5$ if a class interval of more than one tree per class is used. In this case all the tests must be changed to the continuous case which is described later.

Tests of Significance

It is possible to test the significance of difference between two or more sample distributions with respect to skewness and central tendency.

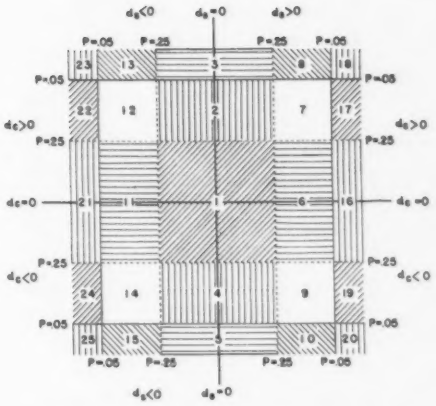

FIGURE 4. *Key to the classification of distributions.*

1. Standard central tendency and symmetry predominant. 2. Predominant positive central tendency, symmetry predominant. 3. Significant positive central tendency, symmetry predominant. 4. Predominant negative central tendency, symmetry predominant. 5. Significant negative central tendency, symmetry predominant. 6. Standard central tendency, positive skewness predominant. 7. Predominant positive central tendency, positive skewness predominant. 8. Significant positive central tendency, positive skewness predominant. 9. Predominant negative central tendency, positive skewness predominant. 10. Significant negative central tendency, positive skewness predominant. 11. Standard central tendency, negative skewness predominant. 12. Predominant positive central tendency, negative skewness predominant. 13. Significant positive central tendency, negative skewness predominant. 14. Predominant negative central tendency, negative skewness predominant. 15. Significant negative central tendency, negative skewness predominant. 16. Standard central tendency, positive skewness significant. 17. Predominant positive central tendency, positive skewness significant. 18. Significant positive central tendency, positive skewness significant. 19. Predominant negative central tendency, positive skewness significant. 20. Significant negative central tendency, positive skewness significant. 21. Standard central tendency, negative skewness significant. 22. Predominant positive central tendency, negative skewness significant. 23. Significant positive central tendency, negative skewness significant. 24. Predominant negative central tendency, negative skewness significant. 25. Significant negative central tendency, negative skewness significant.

An investigator having samples from two plant communities may wish to determine, at a specified probability level, whether the parent populations are the same or different with respect to skewness, central tendency, or both.

The following sets of hypothetical data from two distributions are provided to illustrate the procedures.

Distribution I has a cumulative relative frequency of 0.540 (p_{s_1}) from 0 to $\bar{x} + \frac{1}{2}$, and a relative frequency of 0.240 (p_{c_1}) over the mean class ($\bar{x}$ to $\bar{x} + 1$), with sample size of 100 (n_1), while distribution II has: $p_{s_2} = 0.720$, $p_{c_2} = 0.070$ and $n_2 = 150$. The computations of p_s and p_c from the original frequency distribution data are the same as previously. The two difference tests follow:

Difference due to skewness.

$$k = \frac{|p_{s_1} - p_{s_2}|}{\sqrt{\frac{p_{s_1}(1 - p_{s_1})}{n_1} + \frac{p_{s_2}(1 - p_{s_2})}{n_2}}}$$

$$= \frac{|0.540 - 0.720|}{\sqrt{\frac{0.54 \times 0.46}{100} + \frac{0.72 \times 0.28}{150}}}$$

$$= \frac{0.180}{0.0619} = 2.908, \text{ when } n_1 \text{ and } n_2 \text{ are each} \geq 30.$$

From a table of the normal curve function (Treloar, 1951), $k = 2.908$ has $P < 0.01$. Therefore, the difference in skewness between these two distributions is highly significant; distribution II tends to have more positive skewness, or in terms of the tree association on the ground, II has a greater variation of tree spacing.

Difference due to central tendency. The procedures used are the same as those used in the skewness test, as follows:

$$k = \frac{|p_{c_1} - p_{c_2}|}{\sqrt{\frac{p_{c_1}(1 - p_{c_1})}{n_1} + \frac{p_{c_2}(1 - p_{c_2})}{n_2}}}$$

$$= \frac{|0.240 - 0.070|}{\sqrt{\frac{0.240 \times 0.760}{100} + \frac{0.070 \times 0.930}{150}}}$$

$$= \frac{0.170}{0.045} = 3.579$$

Similarly from a table of k, $P < 0.01$, therefore, the difference in central tendency between these two distributions is highly significant and II tends to more clumpiness of the trees on the ground.

Qualitatively it may be said that the populations from which these samples were drawn are in all likelihood different with respect to skewness and central tendency, II being more clumpy and having a greater variation of tree spacing than I.

Application for Continuous Distributions

The above methods apply to the discrete variable case, where for example, individual trees comprise the population and no fractions or multiples of trees are permitted. However, the continuous variable case, for example when estimating the distribution of basal area or in grouping numbers of trees into classes, may be accounted for by adjusting each test as follows:

Skewness test. The cumulative probability from 0 to $\bar{x}$ is used for testing instead of 0 to $\bar{x} + \frac{1}{2}$.

Central tendency test. The relative frequency over the mean class is computed from the class of $\bar{x} - \frac{1}{2}$ to $\bar{x} + \frac{1}{2}$, and

$$p_E = \frac{1}{2\bar{x}} \text{ instead of } \frac{1}{2\bar{x} + 1}$$

In Fig. 3, the lower x axis should be used as is indicated, the table and key remaining unaltered.

Statistical Basis of the Tests

Let X be a random variable representing the number of trees present on each sampling area unit and f(x) be the probability density function (p.d.f.) of the random variable X. The X is any discrete positive integer with an upper limit, l. Since each sampling unit has a prescribed area, l will be restricted by the number of trees which can occupy that area.

Then $f(x) = P(X = x_i)$, $x_i = 0, 1, 2 \ldots l$.

When $f(x) = k$ (a constant), the distribution is rectangular in relation to any given size of sample unit (s.u.).

If μ, the average number of trees per s.u., is given, then l, k and f (x) can be computed (Figure 5).

$$\text{Let } F(x_i) = \sum_{x_i=0}^{l} (x_i)$$

$$= (l+1)k = 1$$

$$k = \frac{1}{l+1} \quad \ldots\ldots\ldots\ldots (1)$$

$$\text{and } E(x) = \mu = \sum_{x_i=0}^{l} [x_i f(x_i)] =$$

$$k \sum_{x_i=0}^{l} x_i = \frac{kl(l+1)}{2} \quad \ldots\ldots\ldots\ldots (2)$$

Solving (1) and (2): $l = 2\mu$, $k = \frac{1}{2\mu+1}$

$$\text{and } f(x) = \frac{1}{2\mu+1}.$$

The moments with respect to μ are:

$$\mu_1 = E(X-\mu) = \sum_{x_i=0}^{2\mu} [(x_i-\mu) f(x_i)]$$

$$= 0$$

$$\mu_2 = E(X-\mu)^2 = \mu_2' - \mu^2 =$$

$$\sum_{x_i=0}^{2\mu} [x_i^2 f(x_i)] - \mu^2 = 1/3\,(\mu^2+\mu)$$

$$\mu_3 = E(X-\mu)^3 = \sum_{x_i=0}^{2\mu} [(x_i-\mu)^3 f(x_i)]$$

$$= 0$$

Because $\mu_1 = \mu_3 = 0$ and $f(x) = k$, the rectangular distribution is, (1) symmetric with reference to μ, and, (2) the probability of the mean class, μ to $\mu + 1$, is the same as all other classes. Due to the first property the skewness = 0. When the second property is true the central tendency with respect to the rectangular distribution will be termed zero, i.e., when there is no peak or saddle-shape around μ.

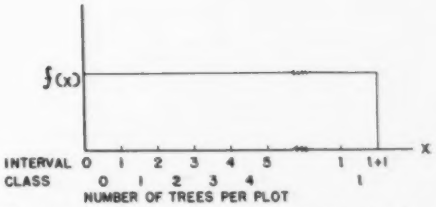

FIGURE 5. *Discrete rectangular distribution indicating intervals and classes.*

There are many possible tree distributions which differ from the standard (rectangular distribution due to varying degrees of skewness and central tendency.

In sampling from a given population, the sampling distribution may be used to predict the degree to which the parent population is different from the standard or rectangular distribution, in terms of probability with respect to skewness and central tendency. Two tests are suggested:

Skewness Test

A null hypothesis is made that skewness = 0. Given n, $\bar{x}$ and n_1 which is the cumulative frequency of the classes from 0 to $\bar{x} + \frac{1}{2}$,

$$\text{then } p_o = P\,(0 \leq X \leq \bar{x} + \tfrac{1}{2}) =$$

$$F(\bar{x} + \tfrac{1}{2}) = \frac{n_1}{n}$$

and p_o is an acceptable measure of skewness. In a rectangular distribution $p_o = \frac{1}{2}$ (symmetry) and a tendency to positive or negative skewness is indicated where $p_o > \frac{1}{2}$ or $p_o < \frac{1}{2}$, respectively.

The significance of the departure from $P_E = \frac{1}{2}$ is measured by the corresponding t value, where

$$t = \frac{p_o - 1/2}{\sqrt{\frac{1/2(1-1/2)}{n}}}$$

(where the single-tailed t value is used as the criterion).

Table 1 showing the values of the departures at P = 0.05 and P = 0.25 for different sample sizes has been computed for convenience, by use of the following formula:

$$d_s = \frac{t}{2}\sqrt{\frac{1}{n}}$$

which is derived from the preceding formula. Any observed distribution may be classified as one of the following according to skewness:

$$(1)\ d_s > \frac{t_{.05}}{2}\sqrt{\frac{1}{n}},$$

skewness is significant, and is positive when $p_o > 1/2$, or negative when $p_o < 1/2$,

$$(2)\ \frac{t_{.05}}{2}\sqrt{\frac{1}{n}} > d_s > \frac{t_{.25}}{2}\sqrt{\frac{1}{n}},$$ skewness is

predominant, and is positive when $p_o > 1/2$, or negative when $p_o < 1/2$,

$$(3)\ \frac{t_{.25}}{2}\sqrt{\frac{1}{n}} > d_s,$$ symmetry predominant.

Fisher (1930), used g_1 to test skewness against the normal distribution. Pearson (1936) and Williams (1935) studied the distribution of g_1 in small-sized samples and derived a table of $\sqrt{b_1}$ showing the values at the P = 0.05 and P = 0.01 levels to test the significance of g_1. However, the g_1 and $\sqrt{b_1}$ tests tend to overestimate skewness in cases of negative central tendency, while the skewness in positive central tendency cases tends to be underestimated in testing against a rectangular distribution. On the other hand, the binomial method gives an unbiased measure of skewness in both the negative and positive central tendency cases, hence it is to be preferred.

Central Tendency Test

The central tendency test depends upon the departure of the observed probability of the mean class $\bar{x}$ to $\bar{x} + 1$ from $p_E = \frac{1}{2\bar{x} + 1}$, the expected value of the mean class in a rectangular distribution.

As in the skewness test, and substituting $\frac{1}{2\bar{x} + 1}$ for p_E,

$$t = \frac{p_o - \frac{1}{2\bar{x} + 1}}{\sqrt{\frac{\left(\frac{1}{2\bar{x}+1}\right)\left(1 - \frac{1}{2\bar{x}+1}\right)}{n}}},$$

where p_o equals the observed relative frequency over the mean class.

Let the departure due to central tendency $= d_c = p_o - \frac{1}{2\bar{x} + 1}$, and from the above equation, a given d_c will have a corresponding t value, the probability of which may be found from the single-tailed t-table (Mood, 1950).

Fig. 3, has been constructed to show the values of the departures at P = 0.05 and P = 0.25 by use of the following formula:

$$\text{Tabular } d_c = p_o - \frac{1}{2\bar{x} + 1} = \frac{t}{2\bar{x} + 1}\sqrt{\frac{2\bar{x}}{n}}$$

which is derived from the t formula above.

A classification of possible observed distributions according to central tendency may be used, similar to that for skewness, as follows:

(1) $d_c > P = 0.05$ tabular value, central tendency is significant and is positive

when $p_o > \frac{1}{2\bar{x}+1}$ or negative when $p_o < \frac{1}{2\bar{x}+1}$.

(2) $P = 0.05$ tabular value $> d_c > P = 0.25$ tabular value, central tendency is predominant, and is positive when $p_o > \frac{1}{2\bar{x}+1}$, or negative when $p_o < \frac{1}{2\bar{x}+1}$.

(3) $d_c < P = 0.25$ tabular value, standard central tendency predominant.

Summary

The method outlined is designed to provide a means of consistently classifying spatial tree associations by areal plots in relative terms of the probable departure of skewness and central tendency from a rectangular distribution, which is used as a standard. The distribution classes obtainable depend on the size of plot used and the association of trees on the ground; so long as the plot size is constant, the relative distribution classes obtained will be consistent. Two tests are involved, one for central tendency and one for skewness, which indicate relative clumpiness of stems in the forest and relative spacing within clumps, respectively. With slight changes the method may be applied to continuous distributions such as basal area. Furthermore, differences between skewness and central tendencies may be found in order to compare similarity of parent populations.

A number of possible applications of the method are apparent in both forestry and botany. Forest and plant ecologists may find it useful in further describing ecological associations; silviculturists could use it to further describe not only how many seedlings survived or are present on an area, but also to a larger degree *how* they survived spatially or are present. Forest managers could use the method to describe basal area distributions of importance in thinning and logging decisions. Simply applying this method, *per se*, will not provide answers to problems since it establishes only relative classifications. But it does permit experience to be associated with these consistent distribution classifications, where the term "distribution" implies nothing more than probability classifications of skewness and central tendency, and where clumps of trees, being considered as units, are not stratified. When they are stratified, it is possible to arrive at the same distribution classification for two populations of stems which have a different association of clumps on the ground and are therefore not homogeneous. An example of this is the case where a density gradient may occur in one population, while in a second population it may be absent, even though the frequency of clumps and more open spaces is the same in each. Presumably such a phenomenon as tree density gradient could be tested by examining the qualities of serial correlation, which would simply further qualify the tests already suggested, as would such other qualifiers as dominance or density as presently used in ecological studies.

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Effect of Precipitation and Temperature on Increment of Yellow-poplar

BY
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OBSERVATIONS of annual rings of trees indicate that, for a short period at least and often for an extended period, the width of the rings are relatively uniform. However, ring growth in a tree may vary with age, suppression, or release. In some areas year-to-year variations are found in width of tree rings within a few years' span which suggests that other factors, possibly substantial yearly climatic changes or differences in monthly climatic changes between years, play a dominant role in influencing the size of the individual rings. Yearly variations in height increment have also been observed, though less frequently, and seem to be less pronounced than ring-width variations.

A yellow-poplar (*Liriodendron tulipifera* L.) stand near Morgantown, West Virginia, was observed by Tryon and Myers (1952) in which many of the yellow-poplars showed a year-to-year variation in ring widths. They attempted to relate annual radial increment with precipitation for selected periods and found that May-June precipitation of the current year gave a significant positive correlation.

Since this study was made, an opportunity has arisen to broaden the scope of the investigation for the same area. An attempt has been made to determine (a) if ring widths are related to periodic temperatures as well as periodic precipitation, (b) if annual height increment is related to periodic precipitation or temperature periods, and (c) whether annual radial or height increment is the more responsive to variations in precipitation and temperature.

Review of Literature

Considerable research has been done attempting to relate periodic climatic factors, especially precipitation, to annual diameter increment of trees growing on areas where year-to-year variation in ring widths had been observed. Far less work, however, has been done in attempting to relate the climatic factors to annual height increment. The factors, and their interactions affecting growth, are so numerous that it is often difficult to isolate the one, or ones, having the greatest influence. The same factors will not always be related to increment on different sites, because those

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factors most nearly limiting would be expected to have the most pronounced effect.

Annual radial increment on sites which are periodically below optimium soil moisture has been directly related to precipitation during or within the growing season by the majority of workers in the eastern United States. Diller (1935), Goldthwait and Lyon (1937), Lodewick (1930), Lyon (1936, 1943), McInteer (1947, 1950), Stewart (1913), and Tryon and Myers (1952) reported a total of 8 species in 7 eastern states from Vermont to Florida in which a positive relationship was found between tree-ring increment and precipitation during the summer months.

In the South, Coile (1936) found a positive relationship between average April-June rainfall and radial growth of shortleaf pine (*Pinus echinata* Mill.). However, radial growth of loblolly pine (*Pinus taeda* L.), slash pine (*Pinus elliottii* Engelm.) and longleaf pine (*Pinus palustris* Mill.) were positively related to winter and spring precipitation. He found a negative relationship between January-May temperature and ring width for loblolly pine, and a similar relationship between June-August temperature for slash pine and longleaf pine.

Several studies from Indiana also have contributed information. Miller (1950, 1951) studying four hardwood species found that rainfall periods during the entire or early part of the growing season were positively related to radial increment. Also, ring widths at the top of the bole gave better correlations with precipitation than those near the base. Kleine *et al.* (1936) reported widths of annual rings of four species of oaks to be correlated directly with June-August precipitation, and inversely with June-August temperature. Precipitation showed a better relationship to ring width than did temperature. Diller (1935) repored an inverse relationship between ring width and mean June temperature for American beech (*Fagus grandifolia* Ehrh.).

Two other works of special interest from the same State are those of Friesner and Friesner (1941) and Friesner (1950). The ring widths of several hardwood species were found to be directly related to precipitation during, or within, the growing season. The latter study, made on a drier site than the former, gave better relationships.

For red pine (*Pinus resinosa* Ait.) in Michigan, Dils and Day (1952) reported a positive relationship between ring widths and summer precipitation, but found temperature to be less closely related. The importance of soil moisture was stressed and it was pointed out that a period of 10 days without rainfall diminished radial increment.

Robbins (1921) studying the growth of oaks in Missouri found that the width of annual rings was correlated directly with March-June precipitation, and inversely with May-June temperatures.

Stephens and Spurr (1947), working with red pine, found that relative humidity as well as rainfall was directly related to daily fluctuations in radial growth. However, an inverse relationship between ring width and air temperature was obtained.

The effect of certain climatic factors on radial increment of trees in the dry Southwest has been summarized by Schulman (1942). He indicated a direct relationship between ring width and October-June precipitation for 5 representative areas. Annual temperature variations were not related to ring widths.

In areas where annual radial increment has been found to be related to precipitation during or within the growing season, as in the eastern United States, excess or deficiency of preciptiation may have a pronounced effect on increment the next year. Diller (1935) found that drought years caused a reduction in radial increment of beech the following year. Robbins (1921), studying the radial increment of oaks in Missouri, found that extremely low precipitation the last part of the growing season in most cases caused a narrow ring the following year. Bogue (1905) studied

growth of annual rings of several species of trees in Michigan. He found that abnormally high precipitation increased ring growth the following year, but abnormally low precipitation reduced ring growth.

In Europe, reduction in size of the annual rings of both conifers and hardwoods because of summer droughts has been reported. Büsgen and Münch (1929) stated that Wiedemann's studies in the middle and lower elevations of Saxony show a reduction in the ring width of spruces and pines caused by repeated summer droughts.

Annual radial increment on moist or cool sites has been studied, but reports of such work are fewer than similar ones on drier sites; and the results appear less definite.

MacDougal (1933) studied the radial growth of Monterey pine (*Pinus radiata* D. Don) growing on the margin of a swamp where moisture was at least adequate at all times. He found greatest radial increment when a maximum amount of sunlight and deficient rainfall occurred during the same season. Antevs (1925) reported that high soil moisture accompanied by cool weather checks radial growth over most of the temperate region during rainy summers.

In northern Finland Hustich (1948) found July temperatures to be directly related to ring width of Scotch pine (*Pinus sylvestris* L.). In southern Finland Laitakari (1922) found a direct relationship between April temperature and ring width. He pointed out that a warm spring initiates diameter growth earlier than normal, which results in a longer growing season and a wider annual ring. No definite relationship was found between precipitation and ring width.

Summarizing work in Europe, Büsgen and Münch (1929) noted that annual diameter increment has been found to depend upon weather conditions of the current growing season. They concluded that "The strongest influence in changing the breadth of annual rings is exerted by those factors of climate which, in a given locality, differ most widely from the optimum—in the north the temperature, in our and more southerly lowland the moisture."

Annual height increment on dry sites, as affected by periodic climatic conditions, was studied by a few workers in the United States early in the present century. They found, in general, that spring precipitation was related to height increment on dry sites.

A close relationship between annual height increment and April-May precipitation was obtained by Pearson (1918) on sapling ponderosa pines (*Pinus ponderosa* Laws.) in Arizona. This investigation revealed no close relationship between air temperatures and annual height increment. Pearson does point out, however, that "There are sites within the range of western yellow pine in this region in which height growth apparently is independent of precipitation. An investigation of these sites would probably show that the moisture supply is normally abundant and that heat is the controlling factor."

Korstian (1921) studied annual height increment of young ponderosa pine and Douglas-fir (*Pseudotsuga taxifolia* (Poir.) Britt.) in an area in Idaho having a 26-inch annual precipitation. He found a close relationship between annual height increment and April-May precipitation, as did Pearson in his work.

In another study, Kirkwood (1914) claimed that annual height increment was closely related to precipitation during the preceding season. He worked with ponderosa pine 30 feet high growing in an area in Montana having an annual precipitation of 16 inches.

Kirkwood theorized that, other things being equal, the length of the shoot depends upon the size and vigor of the buds formed the preceding season, therefore, the past season's climatic factors were of major importance. This point of view was criticized by Korstian (1921), who also claimed that Kirkwood's data bear out Pearson's conclusions as well or better than

his own. That is, that annual height increment is related to current April-May precipitation rather than that of the preceding season. Further study of Kirkwood's data indicates that this criticism was entirely justified.

Motley (1949) in studying the relationship of height with rainfall in Indiana, considered the past May-November precipitation period to be best related to height increment for white pine (*Pinus strobus* L.). A poorer relationship was found for red pine.

Cieslar (1907), working with Norway spruce (*Picea abies* (L.) Karst.) on a dry, stony soil in southern Germany, claimed that deficient summer precipitation results in reduced height increment the following year. The study, however, was based on observations over a very short period.

Annual height increment on moist sites has been studied in Europe. Laitakari (1922), working with Scotch pine in southern Finland, found that the past June temperature showed the highest positive correlation with current height increment. Hustich (1948) found July temperature of the previous season to be directly related to annual height increment in northern Finland.

Büsgen and Münch (1929) reported work by Hesselman in Sweden in which it was found that warm, dry years have a favorable effect on height growth the following year in cool, moist climates.

Other factors than precipitation and air temperature affecting annual height increment have been reported by other workers. These include: number of sunny days (Brewster, 1918), May-June soil temperature at a 6-inch depth (Hiley and Cunliffe, 1922), and length of preceding growing season (Romell, 1925).

Annual height—diameter increment relationships were found to be sparse in the literature. Glock (1937) compared the relationship between annual height increment and ring width of a radially sensitive ponderosa pine growing on a climatically and topographically dry site in Arizona. The relationship was found to be of a "high order," with ring width generally being related directly to annual height increment. As ring width in the area is related to precipitation of the preceding winter, this suggests that annual height increment also is directly related to the precipitation of the same period.[1]

MacDougal (1938) made detailed studies of height and radial increment of Monterey pine growing on dry soils of the Pacific coastal slopes of middle California. He indicated that low correlations were found between yearly increase in height and radial growth of trunks and branches. Shipman and Rudolph (1954) compared annual height and radial growth of two 15-year-old yellow-poplar stands in Michigan with precipitation, using cumulative growth and precipitation values. The cumulative radial and height growth were both highly correlated with cumulative growing-season precipitation for the better stand. In the poorer stand, height growth-precipitation gave a higher correlation coefficient than radial growth-precipitation. They pointed out, however, that stand closure and competition during the last few years of the study presumably lowered the radial growth-precipitation relationship.

Nakashima (1924) studied height and diameter increment of a single 50-year-old fir (*Abies mayriana* Miyabe and Kudo) on a dry site in Japan. A positive relationship was found between annual height and diameter increment. Response of height and diameter growth, but not specifically annual increment, to soil fertility is commented upon by Baker (1950). He suggested that diameter growth may be more affected than height on good sites.

The following statements are a summary of the pertinent points adduced in reviewing the literature where year-to-year

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[1]This suggested relationship was pointed out in correspondence from Dr. Edmund Schulman of the Tree-Ring Laboratory, University of Arizona, Tucson.

variation in tree increment, especially as caused by climatic factors, has been reported:

A. *Annual radial increment*

(a) In eastern United States precipitation within the growing season is the climatic factor most commonly related to annual radial increment. This increment generally is directly related to precipitation. Temperature is less likely to show a relationship, but where one occurs, summer temperatures generally are inversely related to increment.

(b) Extremes in amount of precipitation, particularly during the latter portion of the growing season may influence ring width the next year. Droughts tend to reduce radial growth the next year, whereas excess precipitation increases growth.

(c) On dry sites in southwestern United States, precipitation from October to June, prior to and during the early growing season, has been shown to be related to current radial increment. Temperature has shown no such relationship.

(d) On highly moist sites in western United States, ring widths have been shown to be increased by low rainfall and maximum sunlight.

(e) In continental Europe, reported studies indicate that climatic conditions of the current year are related to ring widths. Summer temperatures have shown a direct relationship on the cooler, moist sites, and summer droughts have caused narrow rings in other areas.

B. *Annual height increment*

(a) In dry areas of western United States April-May precipitation of the current year has been shown to be related to annual height increment. Temperature relationships are weaker.

(b) In continental Europe climatic factors such as precipitation, temperature, and length of growing season of the preceding year have been found related to annual increment.

C. *Annual height — radial increment* Few studies were found which compared the relationship between annual height and annual radial increment. Both good and poor relationship were reported.

Present Study

Description of Area. The study was undertaken on an area of approximately three acres near Morgantown, West Virginia. The area lies at an elevation of 1,100 feet, slightly higher than Morgantown. The mean annual precipitation for Morgantown is 40.61 inches (U. S. Dept. Agri., 1941), being well distributed throughout the year. However, wide departures from the average are not uncommon. During the 20-year period used in this study, annual precipitation varied from 25.15 inches to 53.46 inches. June precipitation during the same period ranged from 2.04 inches to 13.36 inches (U. S. Weather Bureau, 1929-1949).

The mean annual air temperature during the same period was computed to be 53.16°F., with variations from 51.47°F. to 55.34°F. June temperatures for this period varied from 67.5°F. to 75.4°F. Thus variations in precipitation from year-to-year and from June of one year to June of other years are considerably greater in amplitude than are variations in temperature. Considerable variations in temperature and precipitation also occur between the same months of the different years.

The area has a northwest aspect with a 30 percent slope. The geologic strata are composed largely of shales with inter-

bedded sandstones, and date from the latter part of the Pennsylvanian Period. A residual soil, Gilpin loam, has formed from the shales and sandstones. Depth of the soil body to bedrock varies from 2 to 4 feet and drainage, even in the C horizon, is apparently excellent.

Thirty-year-old yellow-poplars predominate in the overstory which also includes red oak (*Quercus rubra* L.), black oak (*Quercus velutina* Lam.), chestnut oak (*Quercus prinus* L.), red maple (*Acer rubrum* L.), and American beech. The quality of the site is rated average for yellow-poplar.

Methods. Nine yellow-poplars which showed year-to-year variation in ring width were selected in 1950 and used to study annual radial increment. These were either in the dominant or codominant crown-classes, free from injury, and showed no evidence of suppression throughout the 30 years that they had been growing. Five additional yellow-poplars were selected from the same area in 1952 for use in studying height increment. The same basis was used in selection of these trees, including the year-to-year variation in radial increment.

Increment cores were taken at d.b.h. on the north and south sides of the 9 trees used in the radial increment study. The width of each ring was then measured to the nearest tenth of a millimeter with the aid of a binocular scope. Averages of each year were used. A 20-year period, from 1930 to 1949, was selected so that reduced radial growth, if existing at the center, would not affect the mean growth trend.

The 5 trees used to study height increment were felled, cut into 4- to 8-foot lengths, and taken to the laboratory. There each length was sectioned through the pith and the annual height increment measured for the same 1930 to 1949 period as used in the radial-increment study. Determination of the end of one year's growth and beginning of the next at first presented a problem. However, by using three criteria

FIGURE 1. *Radial section through the pith of a yellow-poplar stem. Arrow indicates point of completion of one years growth and start of next.*

the authors feel sure that they were able to obtain accurate measurements. These three criteria follow:

(a) A woody constriction is found in the pith at the end of a season's growth.

(b) The pith has plates at the end of a season's growth which generally are coarser than at the beginning of the next.

(c) The annual ring formed next to the pith narrows and finally ends when the season's height increment ceases.

The woody constriction was found to be the most reliable; the other two were helpful but not infallible. The end of a season's height increment is shown in Figure 1.

The first analysis made was for the purpose of studying the variations between individual trees in (a) annual radial increment, and (b) annual height increment. Graphs of the annual radial and height

TABLE 1. Correlation coefficients contrasting the variation in annual radial increment for all trees. One asterisk indicates that the correlation coefficient was significant at the 5 percent level; two asterisks indicate that the correlation coefficient was significant at the 1 percent level.

Tree Number	1	2	3	4	5	6	7	8	9
1	.....	0.387	0.688**	0.576**	0.613**	0.947**	0.155	0.693**	0.586**
2		.....	0.474*	0.628**	0.607**	0.517*	0.195	0.328	0.344
3			.....	0.740**	0.736**	0.854**	0.007	0.840**	0.719**
4				.....	0.804**	0.661**	0.096	0.693**	0.649**
5					.....	0.654**	0.109	0.612**	0.702**
6						.....	0.025	0.755**	0.872**
7							.....	0.117	0.167
8								.....	0.786**
9									.....

increment are shown in Figure 2. To determine whether annual radial increment for each tree showed a similar pattern from year-to-year, comparisons were made between all 9 trees using Galston's correlation coefficient (Snedecor, 1950). In a similar manner data for annual height increment were analyzed for the 5 trees measured.

When annual height increment data were plotted over age, it was evident that height increment had slowed up after the twenty-third year. Consequently, the height data were adjusted to give a linear relationship with age to facilitate regression analysis. The trend for annual radial increment was linear and no adjustment was needed.

The following climatic factors were then related to annual radial increment and to annual height increment, and the significance tested by multiple regression:

(a) Current May-June precipitation.
(b) Current May-June mean annual temperature.
(c) Last season's July-September precipitation.
(d) Last season's July-September mean annual temperature.
(e) Interaction of precipitation vs. temperature for current May-June.
(f) Interaction of precipitation vs. temperature for past July-September.

Both current and past season's precipita-

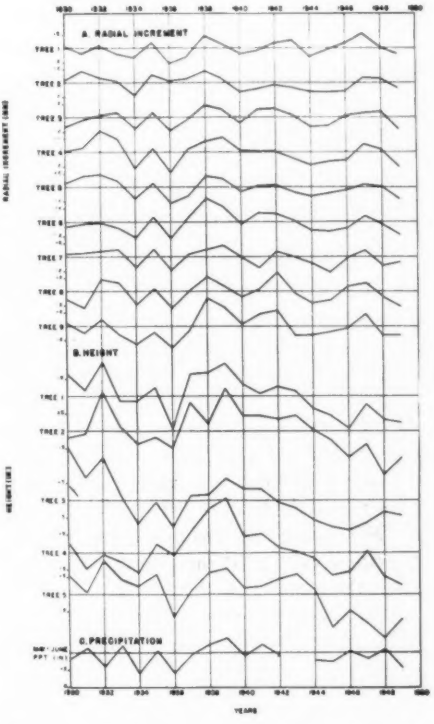

FIGURE 2. *Year-to-year variation in radial increment, height increment, and May-June precipitation. The height increment represents actual values before being adjusted to give the linear trend used in the multiple regression.*

TABLE 2. Correlation coefficients contrasting the variation on annual height increment for all trees. One asterisk indicates that the correlation coefficient was significant at the 5 percent level; two asterisks indicate that the correlation coefficient was significant at the 1 percent level.

		Tree Number				
		1	2	3	4	5
Tree Number	1	.....	0.835**	0.809**	0.738**	0.827**
	2		.....	0.594**	0.742**	0.865**
	3			.....	0.470*	0.650**
	4				.....	0.625**
	5					.....

tion and temperature data were used, as many workers have found one or the other of these closely related to annual increment. July-September was chosen for the period used for the past year as this would be the time of maximum food storage and bud development. Current May-June precipitation and temperature periods were chosen as May-June is the period of maximum growth during the growing season, and May-June precipitation has already been shown to be related to annual radial increment of yellow-poplar in the area.

Results. The year-to-year variations in radial increment between individual trees have been presented in Figure 2. The apparent similarity in growth patterns has been further verified by statistical correlation. The correlation coefficients are presented in Table 1.

The relatively high number of significant correlations indicate that most of the trees showed the same growth pattern from year to year. Tree 7 shows no significant annual correlation in radial growth with any of the other trees. However, Figure 2 indicates that this tree had somewhat the same general trend, although it was apparently less responsive to environmental changes.

The correlation coefficients indicating the variations in annual height increment between individual trees are presented in Table 2.

All 5 trees showed a significant relationship indicating that year-to-year variations in height increment were consistent. This similar growth pattern is apparent in Figure 2. These similar height trends, like those of radial increment, indicate dependence on some environmental factors.

The effect of precipitation and temperature during May-June of the current growing season, and of July-September of the past season were tested to determine whether a relationship existed between these precipitation and temperature periods and annual radial and height increment of yellow-poplar. The relationship was tested for the period 1930 to 1949 by multiple regression analysis. One such analysis was used to test the effect of the precipitation and temperature periods and their interactions on annual radial increment, and a separate one was used to test the effect of those same periods on annual height increment.

Results of these 2 multiple regression analyses are presented in Table 3.

The relationship between May-June precipitation of the current year and annual radial increment proved to be significant at the 1 percent level. This relationship was positive with annual rings tending to be wider with high amounts of precipitation in May-June and narrower with decreased precipitation.

No significant relationship was obtained between the amount of precipitation occurring in July-September of the past season and the current season's annual ring width. Likewise, the interactions of precipitation

TABLE 3. Relationship of climatic factors to annual radial and height increment as determined by multiple regression analyses.

Source of variation	Significance of correlation with Radial increment	Height increment
Current May-June precipitation	1%	None[1]
Current May-June temperature	None	None
Past July-September precipitation	None	None
Past July-September temperature	None	None
Interaction of precipitation vs. temperature for current May-June	None	None
Interaction of precipitation vs. temperature for past July-September	None	None

[1]More nearly significant than the other factors relating to height increment.

vs. temperature for the current May-June, and for the past season's July-September period were not significantly related to annual ring width.

Neither the 2 precipitation periods, the 2 temperature periods, nor the 2 interactions were significantly related to annual height increment, although the highest value of "F" occurred for the May-June precipitation period of the current year.

In order to test further the importance of the precipitation and temperature periods in relation to annual height increment, the method of Kincer and Mattice (1928) was employed. The results of this test showed that the relationship between current May-June precipitation and annual height increment approached significance more closely than the other precipitation and temperature periods. As the relationship was positive, there is, then, a tendency for height increment to increase with high May-June precipitation and to decrease as precipitation is reduced.

To further test the relationship between May-June precipitation and height increment, a regression of annual height increment vs. annual radial increment was used. The regression proved significant at the 1 percent level, showing that a relationship does exist between the two increments, and that annual height increment tends to increase or decrease with ring width. This regression of annual height increment over annual radial increment is shown in Figure 3. It may be expressed as $Y = 13.32 + 2.35X$, where Y = annual height increment in inches, and X = annual radial increment in millimeters.

This significant relationship between annual height increment and annual radial increment strengthens the possibility that a real relationship does exist between May-June precipitation and annual height increment, even though it is weaker than the season, particularly the early part, has a yellow-poplar on the site studied, the amount of precipitation during the growing relationship with annual radial increment. The results of this study indicate that, for direct influence on the width of annual rings. This is in agreement with results of most other studies in the eastern United States where year-to-year variation in ring width has been related to precipitation during the growing season.

Discussion

The amount of precipitation during the early portion of the growing season was found to influence annual height increment more than did the other precipitation and temperature periods studied. However, ring width was more responsive to precipitation than was height increment. The influence of precipitation during the growing

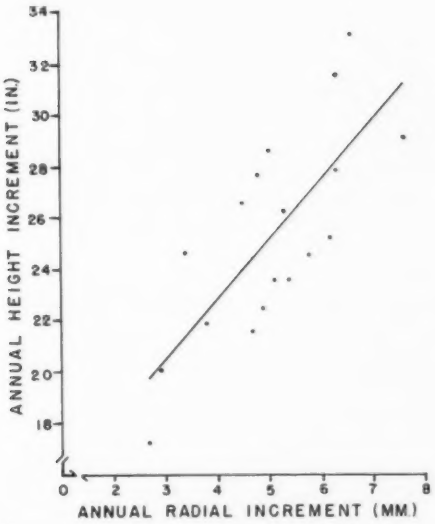

FIGURE 3. *Regression of annual height increment on annual radial increment. The relationship is significant at the 1-percent level.*

season on annual height increment agrees with work in the western United States where year-to-year variation in height growth of conifers on dry sites was found to be influenced by precipitation during the early part of the growing season. However, the relationship between height and precipitation, as found in the West appears closer than that found in the present study. Possibly this difference may be caused by the lower precipitation with the resulting soil moisture being more nearly limiting in the western areas than in the area studied.

The results, however, disagree with European studies of the influence of climatic factors on height increment. There, better relationships were found between climatic factors of the past season and annual height increment than with those of the present season. Thus the European view emphasizes the condition of the tree as a result of amount of food stored the past season, as contrasted with the American view which stresses the importance of environment during the growing season.

In an attempt to explain the reason for the different findings of American and European workers, Hustich (1948) has advanced the following hypothesis: In those parts of the temperate zone where water is always plentiful in the spring, height increment is determined by the weather conditions of the previous summer. Favorable weather conditions in these moist areas involve a combination of high temperatures and low precipitation. These favorable weather conditions result in increased storage of reserve food which influences height growth the following year. However, in well-drained and dry situations where growth is dependent upon current precipitation, as in the southwestern United States, Hustich pointed out that height increment shows a direct relationship to precipitation during the growing season. The references given in this paper show close agreement with the views of Hustich, but his explanation does not seem to be complete or to cover all cases.

Considerable difficulty has been encountered by workers attempting to determine the site factors most closely related to growth. It is a complex problem as pointed out forcibly by Glock (1955).

On areas where year-to-year variation in diameter or height has been observed, workers have reported different site factors such as precipitation or temperature most closely related to annual variation in tree increment. This factor may be precipitation, temperature, or length of growing season. Even the same site factor may be more effective in one portion of the year than another. Precipitation in one area may be most effective during the growing season, but in another area the winter, or even last year's precipitation may be most important.

In America, at least, those factors which affect the amount of soil moisture during the growing season have been the ones most commonly reported as influencing annual variation of both diameter and height increment. That precipitation, and the resulting soil moisture, should be so important

is not surprising. Recent soil-site studies throughout the United States consistently pointed to the importance of physical properties of the soil in affecting tree growth. Furthermore, good physical properties usually indicate favorable moisture-holding capacity of the soil.

Based on the present research and a study of the literature pertaining to relationships between climatic factors and annual increment, the writers present the following statements as their interpretation of increment changes that may be expected in going from a site producing relatively uniform growth to one producing year-to-year variation.

Under conditions which do not deviate too far from optimum, the width of the annual rings and the annual height increment tend to be uniform, at least over a portion of a tree's life, if suppression and age trends are not considered. Such a condition is the usual one found in our forests. As one progresses from optimum to adverse sites, one or more site factors will become limiting. Thus on certain physiographic areas within the optimum range of a species, soil moisture becomes limiting for tree growth, especially in years when precipitation is below normal. On the contrary, excessive soil moisture may decrease soil aeration below that needed for the physiological processes of the roots. This latter condition will be most pronounced when precipitation is high and temperature is low. In both situations, those factors may become limiting to the point that increment of the tree is reduced.

It is also suggested that ring width is more responsive to changes in site than annual height increment. Thus, as a site varies from the optimum the tendency for a site factor or factors to become limiting first shows up in diameter increment while annual height increment tends to remain more uniform. This situation has been shown in the present paper where the ring widths of yellow-poplars are more sensitive to precipitation changes than annual height increment.

Another instance where diameter growth also is more affected than height growth of a tree, is in crowding. Both are affected by restricted growing space, but diameter is influenced to a greater degree than height. Foresters, in determining site quality by the site index method, use tree height because it is less affected by crowding than is diameter growth.

Summary

Yellow-poplar growing on a well-drained hillside, and showing year-to-year variation in ring width, was investigated to determine the effect of precipitation and temperature periods on annual radial and height increment.

May-June precipitation was directly related to ring width. Precipitation for the same period was also related to annual height increment, although the relationship was poorer than for ring width. Temperature for the present and past seasons, and precipitation for the past season, showed no relationship to either annual radial or height increment.

The annual variations in diameter and height increment as one progresses from optimum to adverse sites is discussed.

It is suggested that as a site factor, or factors, become limiting radial increment responds to the change to a greater degree than height increment.

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Some Effects of Various Combinations of Day and Night Temperatures and Photoperiod on the Height Growth of Loblolly Pine Seedlings

BY
PAUL J. KRAMER

ALTHOUGH it is well known that temperature affects growth in a number of ways, few quantitative data are available concerning its effects on tree growth. Reed (1939) measured shoot growth of loblolly pine in the field and concluded that the seasonal course of growth was controlled by air temperature. This is probably true of the resumption of growth in the spring which seems to occur as soon as temperatures become high enough, but it is not true of the cessation of growth which usually occurs in August, long before temperatures are low enough to hinder growth (Reed, 1939; Young and Kramer, 1952). It also is well established that photoperiod affects the length of growing season of loblolly pine (Kramer, 1936; Zahner, 1955), but this cannot be responsible for cessation of growth in late summer because photoperiod is still too long to be limiting. The relationships between growth, temperature, and photoperiod are shown in Figure 1 for a group of two-year old loblolly pine seedlings and several other species growing in the open, based on an earlier study (Kramer, 1943).

It seems possible that the high temperatures of mid-summer might produce internal conditions resulting in the cessation of growth. It also seems possible that the relative day and night temperatures might be a factor. Went (1948, 1953) has shown that the relation between day and night temperatures has marked effects on the growth of various herbaceous species and termed this phenomenon thermoperiodism. A series of experiments therefore was planned to measure the effects of various combinations of day and night temperatures on the growth of loblolly pine (*Pinus taeda* L.) seedlings. Such a study requires accurate control of day and night temperatures combined with light intensities high enough for good growth of pine seedlings. These conditions were provided in the air conditioned greenhouses of the Earhart Plant Research Laboratory (sometimes called the Phytotron) of the California Institute of Technology.[1]

Methods

The seedlings used in these experiments were grown from seeds collected in the eastern part of North Carolina. The seeds were germinated by the staff of the Ear-

[1]The writer wishes to express his deep appreciation of the co-operation given by Professor F. W. Went, Director, and by the entire staff of the Earhart Laboratory in connection with this project. The financial support required for travel, rental of space in the Earhart Laboratory and wages of a technician was supplied by a grant from the National Science Foundation.

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hart Laboratory, and the seedlings were grown there for a year before the beginning of the experiment. The seedlings were grown in quart plastic containers in a mixture of fine crushed rock and vermiculite and supplied regularly with deionized water and a standard nutrient solution. During the first season they were grown with natural illumination in a greenhouse with a day temperature of 23°C. and a night temperature of 17°C. These seedlings grew as well as other seedlings from the same lot of seed which were grown in pots of soil in the Duke University Greenhouses. From December first to early February they were given 16 hours at 4°C. in darkness, daily, to insure breaking dormancy.

On February 10 the seedlings were distributed in groups of eight and subjected to the various treatments. Three daytime temperatures were used, the lowest and highest available in the greenhouses, and an intermediate one. The greenhouses are ordinarily operated at a night temperature 6 to 7 degrees lower than the day temperatures, hence by moving seedlings from one house to another it was possible to obtain 9 different combinations of day and night temperatures. Only 7 combinations were used in this experiment because of lack of space and seedlings. The containers in which the seedlings were growing were kept on trucks so they could be moved easily from house to house. The temperature combinations actually used are shown in Table 1. The day temperatures were maintained from 8 a.m. to 4 p.m. and the night temperatures for the remaining 16 hours of the day. All of these seedlings received natural illumination at an intensity of about half of full sunlight. The values in Table 1 represent the averages of 7 or 8 seedlings except in the group with 23° day and night where only 5 of the original seedlings survived.

Other groups of seedlings were grown with 8 and 16 hour photoperiods at day

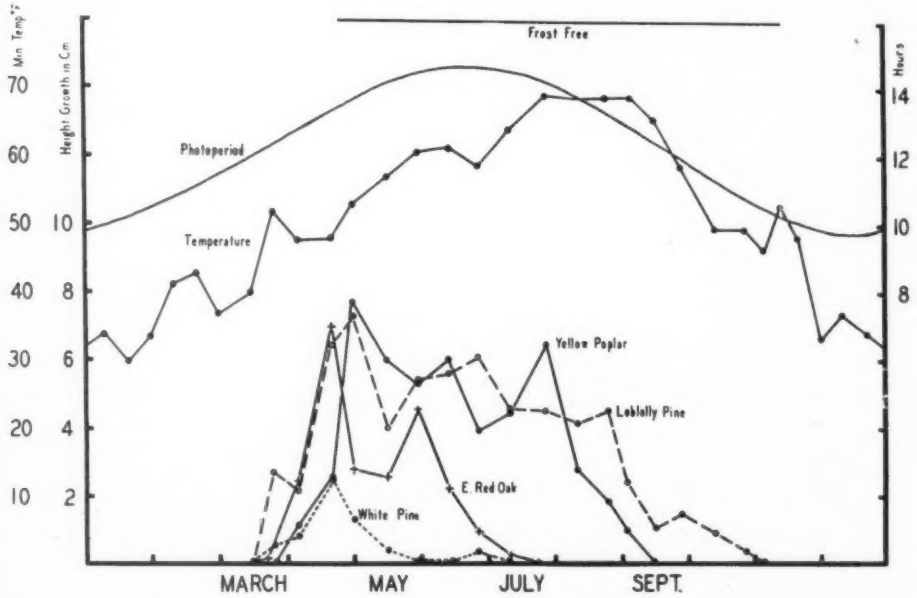

FIGURE 1. *Height growth of 2-year-old loblolly pine seedlings and certain other species in the open, together with minimum temperatures and photoperiod. From data of Kramer (1943).*

TABLE 1. Growth of 1-year-old loblolly pine seedlings with various day and night temperatures over a period of approximately 8 months.

Day temp.	Night temperature 11	17	23
A. Increase in height in centimeters. A difference of 2.8 cm. is significant at the ±5 percent level.			
30	—	33.2	19.9
23	30.2	24.9	15.8
17	16.8	10.9	—
B. The height growth as a percentage of the initial height.			
30	—	106	62
23	97	69	51
17	50	35	—

temperatures of 23°C. and night temperatures of 17°C. Those receiving an 8 hour day were kept in the greenhouse from 8 a.m. to 4 p.m. and then transferred to an air-conditioned darkroom at 17°C. for the dark period. The seedlings receiving a 16 hour photoperiod were kept in the same greenhouse from 8 a.m. to 4 p.m. and then transferred to an air-conditioned room at 17°C. and given 8 hours of artificial light at about 500 foot candles followed by 8 hours of darkness, after which they were transferred back to the greenhouse.

Results

Growth and survival were sufficient at all temperatures and photoperiods to permit statistical analysis of the data and definite conclusions. Out of a total of 56 seedlings, only 6 died, 3 from the group subjected to 23° day and night, 2 from the group with 17° days and 11° nights, and 1 from the group with 30° days and 17° nights. The growth data for the various combinations of temperatures are summarized in two ways in Table 1; the first part showing the total increment in height for the season for each treatment, and the second part the total increments expressed as percentages of the initial heights. The relative rank of the various treatments is the same by both methods

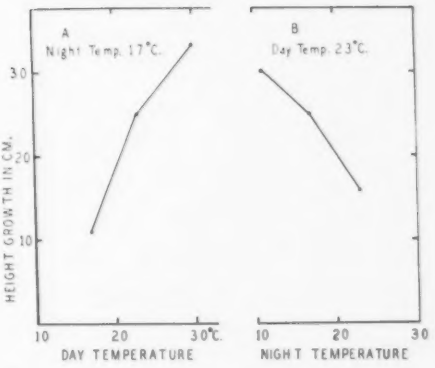

FIGURE 2. *Height growth of loblolly pine seedlings grown with various combinations of day and night temperatures. A shows increased growth with increased day temperatures, when night temperature was 17° C. B shows decreased growth with increased night temperatures when day temperature was 23° C.*

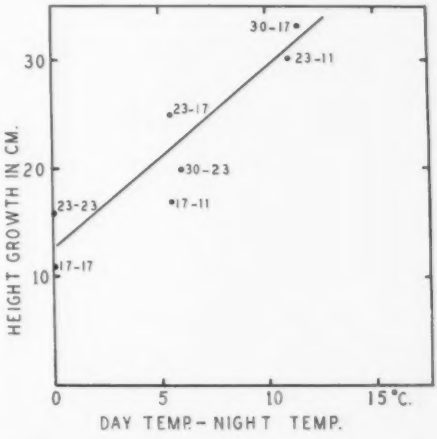

FIGURE 3. *Height growth of loblolly pine seedlings plotted over the difference between day and night temperatures. The pair of numbers beside each point gives the day and night temperatures at which the trees were grown. A large difference between day and night temperatures was most favorable for growth.*

TABLE 2. Growth of loblolly pine, in centimeters during each month of the experiment. Data are averages of 8 seedlings in most experiments.

Temperature		Dates									
Day	Night	2-17 to 3-19	3-19 to 4-16	4-16 to 5-14	5-15 to 6-11	6-11 to 7-16	7-16 to 8-16	8-16 to 9-13	9-13 to 10-29	Growth for Season	Growing Season in Days
30	23	7.8	2.6	2.4	2.4	2.4	1.4	0.9	0.0	19.9*(cm.)*	195
30	17	6.7	3.5	2.6	5.8	8.1	3.9	2.1	0.5	33.2	235
23	23	5.0	4.3	0.0	2.4	1.9	0.9	0.8	0.5	15.8	215
23	17	3.5	9.1	1.4	3.4	3.2	2.7	1.4	0.2	24.9	215
23	11	2.2	7.3	2.4	2.4	7.2	4.3	3.3	1.1	30.2	220
17	11	0.0	2.4	4.2	1.8	1.5	2.9	2.5	1.5	16.8	185
17	17	2.0	2.9	2.1	0.4	1.3	1.4	0.4	0.4	10.9	210

because the groups were quite uniform in height at the beginning of the experiment.

Even casual inspection of the data permits certain conclusions. Growth increased with increasing day temperature and decreased with increasing night temperature, as shown in Table 1 and Figure 2. A day temperature of 17° was too cool for good growth and the highest day temperature used in these experiments was not above the optimum. Best growth occurred with night temperatures 12 or 13 degrees lower than day temperatures and very poor growth occurred in seedlings kept at either 17 or 23° day and night. There was little difference between the total amount of growth made with a 30° day and 17° night and a 23° day and 11° night, suggesting that within certain limits the spread between day and night temperature may be more important than the actual temperatures (see Fig. 3).

Although there were wide variations in amount of growth at various temperatures there was little visible injury, except that the seedlings kept at the lowest day and night temperatures became somewhat chlorotic by May and their older needles began to die. The new growth on these seedlings also bore needles less than half the usual length, but the seedlings continued to grow in spite of their unhealthy

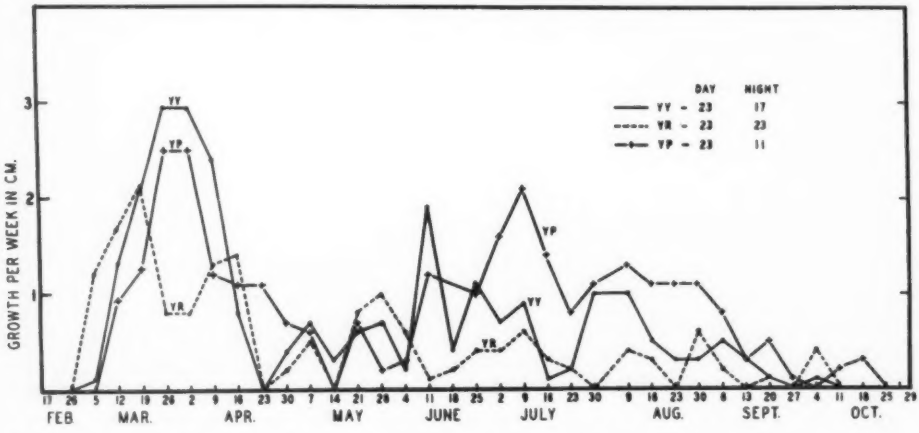

FIGURE 4. *Seasonal course of height growth of 1-year-old loblolly pine seedlings grown with naturally varying length of day, a day temperature of 23° C. and low, intermediate and high night temperatures.*

appearance and only 2 of them died. The importance of the relative day and night temperatures can be seen more clearly when height growth is plotted over the difference between day and night temperatures. As shown in Figure 3, the larger the difference between day and night temperatures the greater the amount of shoot growth. These results indicate that, within the limits of the temperatures used in this experiment, the spread between day and night temperatures is more important than the actual temperatures.

Temperature affected the speed of resumption of growth and the time of cessation, as well as the seasonal distribution, as shown in Table 2 and Figures 4 and 5. The highest temperatures resulted in most rapid resumption of growth at the beginning of the season and most growth during the spring, but they also resulted in less growth after midsummer and earlier cessation of growth than lower temperatures. The most growth late in the summer was made with intermediate or cool days combined with cool nights.

The effects of photoperiod are shown in Table 3 and Figure 6, where it can be seen that a photoperiod shorter than normal reduced both the amount of shoot growth and the length of the growing season, while a photoperiod longer than normal materially increased the amount of growth and the length of the growing season. Seedlings receiving a shorter than normal photoperiod were slower to start gowth in the spring and ceased growth sooner than those receiving either natural photoperiod or a 16-hour photoperiod. Two of the 8 seedlings receiving an 8-hr. photoperiod died. The stimulus of a long photoperiod was especially noticeable in the autumn, and growth with a 16-hr. photoperiod had not ceased completely when the experiment was terminated at the end of October. These results agree with those obtained in previous experiments in which the length of the growing season of loblolly pine seedlings were greatly prolonged by a long photoperiod (Kramer, 1936).

Another interesting observation made in connection with this study was that individual trees seldom grew continuously for more than 5 or 6 weeks. For example, the average height of the group grown with 30° day and 17° night increased every week for 29 consecutive weeks, but in only 3 of these weeks did all 7 of the trees grow. During 18 of the

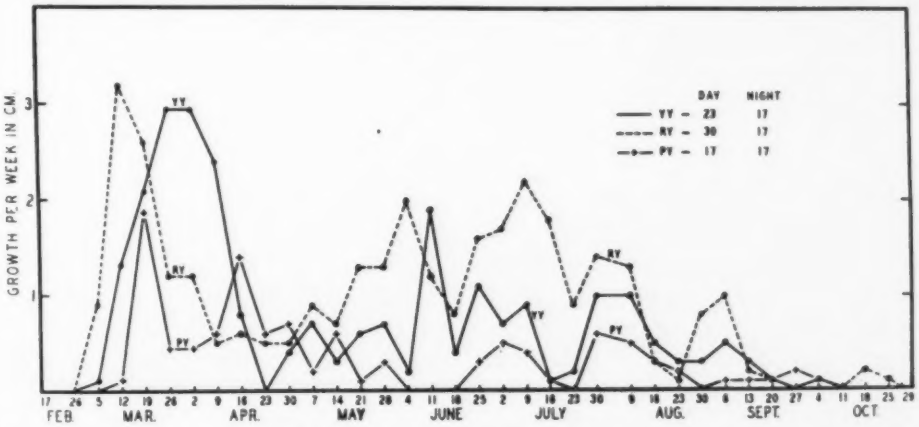

FIGURE 5. *Seasonal course of height growth of 1-year-old loblolly pine seedlings grown with naturally varying length of day, a night temperature of 17° and low, intermediate and high day temperatures.*

weeks less than 5 trees made measurable height growth. Two trees grew for 23 consecutive weeks, but none of the others grew more than half this long without an interruption of growth, and not a single tree in the entire experiment grew continuously from beginning to end of the growing season. Differences in length of the growing periods of individual trees receiving various treatments are shown in Table 4.

TABLE 3. Growth of seedlings with various photoperiods. Day temperature 23°, night temperature 17°C.

Photoperiod	Growth for season	Growth after August 1	Growing season in days
	(*cm.*)	(*cm.*)	
8 hours	14.7	1.2	200
Natural	24.9	3.2	215
16 hours	31.8	8.3	240

Discussion

The results of this experiment are fairly definite, but they raise some questions which are difficult to answer. First in importance is why high day temperatures increase shoot growth and high night temperatures decrease it. Reed (1939) found a close relationship between growth of loblolly and short-leaf pine growing in the field and the physiological temperature index of Lehenbauer, height growth increasing about 1.4 per cent for an increase of one unit in the physiological temperature index. Went (1944) observed that the optimal day temperature for growth of tomato is about 25° C. and attributed this to the high rate of photosynthesis at this temperature. Experiments of Decker (1944) suggest that the optimum temperature for photosynthesis is about 30° C., the same day temperature which resulted in best growth in this experiment. It is doubtful, however, if increased photosynthesis alone can explain the increased growth as the temperature was increased from 17 to 30°, because it appears from Decker's data that photosynthesis would be increased only 20 percent, while shoot growth actually was tripled.

Decreased growth with increased night temperatures has been observed in several other species by Went (1953). He attributed this to decreased translocation of food to the growing regions (Went, 1944), but this is questioned by other investigators (Hewitt and Curtis, 1948;

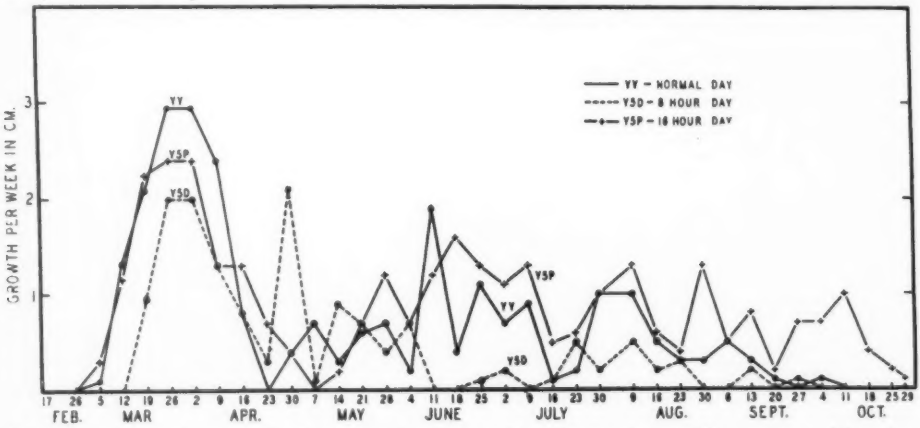

FIGURE 6. *Seasonal course of height growth of 1-year-old loblolly pine seedlings grown with a day temperature of 23° C. and a night temperature of 17° C. and various photoperiods. The trees given a 16-hour photoperiod received 8 hours of natural illumination plus 8 hours of artificial illumination of low intensity.*

TABLE 4. The total number of weeks, out of the 36-week period of observations, in which growth was made by individual seedlings in 3 different temperature treatments, the average number of weeks in which seedlings grew, and the total length of the growing season.

Tree No.	Temperature treatment 30-17°	23-17°	23-11°
1	26	27	17
2	20	4	26
3	29	13	21
4	13	16	26
5	13	20	20
6	Dead	25	25
7	18	18	24
8	20	25	23
Av. number of wks. in which growth occurred	19.8	17.7	22.7
Length of growing season in weeks[1]	34	29	33

[1]Length of growing season is the number of weeks from the time the first seedling in a treatment started growth until the last seedling ceased growth.

Swanson and Böhning, 1951). A more probable explanation is the increased use of food in respiration at higher temperatures. Lundegardh (1931) stressed the importance of low night temperatures in conserving food by reducing its use in respiration. Decker's data indicate that respiration of loblolly pine approximately doubles from 11 to 23°, while in this experiment shoot growth was only about half as great at 23 as at 11° when the temperature was kept at 23° during the day. Nevertheless, it is doubtful if increased respiration alone could account for the reduction in growth.

Careful measurements of photosynthesis and respiration over a wide range of temperatures would permit better evaluation of the roles of these processes in explaining the reaction of loblolly pine seedlings to various combinations of temperature. Such studies are now in progress.

It seems probable that other factors in addition to the manufacture of food by photosynthesis and its use in respiration are involved in the reaction of tree seedlings to temperature. Perhaps growth is partly limited by processes concerned in the utilization of food in forming new protoplasm, or by the rate of translocation to growing regions, rather than by the supply of food. This is indicated by the behavior of seedlings given a 16-hr. day. These seedlings were exposed to daylight of sufficiently high intensity for photosynthesis for 8 hrs., then given 8 hrs. of light at an intensity too low for appreciable photosynthesis. They grew about twice as much as seedlings given only 8 hrs. of sunlight, and significantly more than those exposed to natural photoperiod. This indicates that the seedlings could manufacture sufficient food for normal growth in 8 hrs., and that the increased growth with long photoperiod resulted from more efficient utilization rather than from increased supply of food.

The seasonal distribution of growth of the seedlings also deserves comment. Figures 4, 5, and 6 show a rather similar seasonal pattern of growth in all treatments. It is characterized by rapid growth early in the season followed by a marked decrease or even complete cessation, a second period of rapid growth and then a gradual decline in rate during late July and August. Four of the 7 groups made half of the season's growth during the first 2 months although some growth occurred over a period of about 8 months. This behavior is characteristic of many species when growing in the open. Reed (1939) reported that loblolly and shortleaf pine trees growing in the open made over half of the season's growth before June 15, although growth did not cease completely until early September, and Young and Kramer (1925) found the same situation in 13 year old loblolly pine trees about 35

ft. tall. Kramer (1943) found that several species of hardwood and pine seedlings made most of their growth in the first half of the growing season.

Apparently it is normal behavior for the seedlings to grow rapidly at first, more gradually for a long period of time, and finally cease growth before temperatures are low enough to be limiting. In these experiments the seedlings received adequate water and mineral nutrients at all times and the temperature was maintained at the same level for each group throughout the season. Nevertheless, the seasonal pattern of growth for trees grown in the air-conditioned greenhouses was similar to that for trees growing in the open, as seen by comparing Figures 4 and 5 with Figure 1. Such behavior sometimes is attributed to unfavorable environmental conditions, but this was not true of the seedlings grown in the Earhart Laboratory. The very rapid initial shoot growth consists largely of cell enlargement, but later growth must involve a more complex pattern of activities, including formation of new cells. There usually is an abundance of reserve food available early in the season, but later in the season there is competition for the products of photosynthesis among diameter, shoot and root growth. The midsummer slowing down of growth cannot be attributed to lack of food, however, because it occurs at a time when food is beginning to accumulate. More probably it occurs because of depletion of a growth-promoting substance or accumulation of an inhibitor.

The seasonal pattern was modified somewhat by the temperature treatments, more growth occurring late in the season with cool days and nights, or with nights much cooler than days, and less growth occurring late in the season with the warmest nights and with nights as warm as days. These data suggest that perhaps the warm nights of midsummer not only depress the rate of growth, but also produce internal physiological changes which result in the early cessation of growth observed in many species. Pollock (1953) suggested that oxygen might become limiting to respiration in buds during the high temperatures of late summer and cause accumulation of a growth inhibitor. Vegis (1956) also believes that dormany is caused by oxygen deficiency in buds during periods of high temperature.

Another interesting question, probably related to the seasonal distribution of growth, is why individual trees grow intermittently rather than continuously, even when kept in the uniform environment of the Earhart Laboratory. In this experiment growth was observed over a period of 34 weeks in the group of trees receiving 30° days and 17° C. nights, but in only 3 of these 34 weeks were all of the seedlings of this group growing simultaneously. Two seedlings in this group grew continuously for 23 weeks, but two others grew only 6 weeks before ceasing growth temporarily. The average seedling grew about 20 weeks out of a possible 35 weeks. The total number of weeks in which each individual tree made a measurable increase in height is shown for three treatments in Table 4. The writer has observed similar intermittent growth in several deciduous species including eastern red oak seedlings growing in the Earhart Laboratory. Young (personal communication, 1956) observed intermittent growth in 13-year-old loblolly pine trees growing in a plantation. He observed their growth for 26 weeks, from March 29 to September 20, but none of the 17 trees under observation grew continuously for more than 15 weeks and some grew only 5 to 6 weeks before ceasing growth temporarily. Intermittent growth is common in tropical trees (Coster, 1927, 1928; Klebs, 1915) and it has been studied in tea (Bond, 1945; Wight and Barua, 1955) where 4 or 5 "flushes" or periods of growth occur annually, with intervening periods of dormancy.

In the field these periods of intermittent growth have often been attributed to environmental factors, but this cannot be the

explanation in the Earhart Laboratory where the environment is kept constant. Here it must be caused by some internal factor. Either the trees temporarily exhaust some factor essential for growth, or else they accumulate a substance which inhibits growth. Hemberg (1949) claimed to have demonstrated accumulation of inhibitors in Fraxinus during the onset of dormancy. Pollock (1953) thought that oxygen might become limiting in respiration during the high temperatures of late summer and cause accumulation of an inhibitor.

This and other similar observations emphasize the fact that cessation of growth does not necessarily result in permanent domancy. Apparently trees often cease growth one or more times during the growing season without becoming dormant. Perhaps permanent dormancy only develops after growth has ceased for a certain length of itme and this might vary with environmental conditions. According to this view cessation of growth and development of the dormant condition are separate processes with different causes. This is consistent with the views of Pollock and of Vegis, mentioned earlier, that at high temperatures an oxygen deficit develops in the buds and the resulting anaerobic respiration causes formation of an inhibitor and development of permanent dormancy. Growth might cease and start again several times, but only if conditions were favorable for formation of an inhibitor would it cease permanently. The mechanisms responsible for both temporary and permanent cessation of growth probably are complex, but they are of sufficient practical and theoretical value to deserve careful study.

It should also be pointed out that the reaction of loblolly pine to various combinations of day and night temperatures appears to help explain its geographical distribution. Loblolly pine occurs from the Gulf Coast and northern Florida to southern Tennessee, and in the Coastal Plain, to southern New Jersey. Thus far there has been no satisfactory explanation either for the limits on its southward extension or for the fact that many foresters claim that it makes its best growth on the Virginia-North Carolina line, near the northern edge of its range.

The average day temperature at Raleigh is slightly higher than at Tallahassee, but the night temperature is 1.7° C. lower, hence the difference between day and night temperatures is 2.5° C. greater at Raleigh. This difference seems small, but inspection of the data in Table 1 shows that with a 30° day, height growth was increased 2.2 cm. or 11 percent per degree for each decrease of one degree in night temperature from 23 to 17° C. Thus the greater difference between day and night temperatures at Raleigh could at least theoretically produce an increase in height growth of 27.5 percent above that at Tallahassee. This effect presumably is produced mostly through reduction in respiration, although as mentioned earlier, other processes may be involved.

These results suggest that careful study of day and night temperatures may assist in explaining other problems of plant distribution which cannot be explained by maximum or minimum temperatures. The results reported in this paper suggest that even a small difference in temperature exerted over the entire growing season can produce surprisingly large results in growth. It therefore seems that thermoperiodism can be added to photoperiodism as an important factor in the control of tree growth.

Summary

One-year old loblolly pine seedlings were grown from February to October in the air-conditioned greenhouses of the Earhart Laboratory for Plant Research with various combinations of day and night temperatures and with short and long photoperiods. Height growth was recorded weekly.

When the night temperature was maintained at 17° C. the amount of shoot

growth tripled as the day temperature was increased from 17° to 30° C., but when the day temperature was maintained at 23° the amount of shoot growth was reduced about 50 percent by increasing the night temperature from 11° to 23° C. Best growth was made with the widest spread (12 or 13°) between day and night temperatures and poorest growth with nights as warm as days.

Seedlings grown at the highest temperatures resumed growth sooner and made more growth early in the season than those grown with lower temperatures, but the latter made more growth late in the season. The most late season growth was made by trees grown with the coolest nights, suggesting that the hot nights of mid and late summer may tend to bring about cessation of shoot growth.

Seedlings grown with constant temperatures from February to October showed the same seasonal distribution of growth as trees growing in the open, growing rapidly early in the season and very slowly late in the season. An 8-hr. photoperiod shortened the growing season and a 16-hr. photoperiod prolonged it, but did not change the shape of the growth curve materially.

Individual seedlings growing with a uniform temperature and adequate water and mineral nutrients did not grow continuously throughout the growing season, but intermittently stopped growth and then started again after a few weeks. Only occasionally did all of the seedlings receiving a certain treatment grow at the same time.

The results of this study suggest that loblolly pine may thrive better in the northern than in the southern part of its range because there is a greater difference between day and night temperatures in the northern part. Even a small difference in temperature can produce measurable differences in amount of shoot growth.

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Koestler's Silviculture

Silviculture. By Josef Köstler. English translation by Mark L. Anderson. Oliver & Boyd Ltd., Edinburgh, Scotland. 416 pp. 45 s. ($6.30). 1956.

Review by Stephen H. Spurr
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The appearance of an English translation of a standard German text on silviculture is a noteworthy event. Prof. Köstler (1902-) of the University of Munich completed the German text in 1949, and Prof. Anderson of the University of Edinburgh has added it to the major works which he has translated into English.

The work is a summary of the subject matter of lectures delivered over 140-150 hours during two terms covering both silvics and silviculture. The reader looking for details of German research and practical silviculture will be somewhat disappointed. The work is rather of the nature of an essay presenting the naturalistic concepts of silviculture as evolved in Karl Gayer and the modern school of plant sociology. The book abounds in philosophic quotations and expressions such as "the true path, which starts off from the selection forest" and "Silviculturists under present-day conditions may be called forest nurses and physicians in sick forests."

The organization of the book follows the classical pattern. The first half deals with silvics, including both autecology and synecology. Many topics are dealt with but briefly, such as effects of light (4½ pages) and inherited qualities of trees (5½ pages). Plant sociology, however, particularly that part dealing with the forest associations of southern Germany, is treated at some length. The same can be said for the second half on silviculture. Clearcutting with natural regeneration requires 3 pages and planting methods 7 pages, while thinning and the selection system are given a much more exhaustive and philosophical treatment.

The work is pointed toward south Germany in particular, and surrounding central Europe in general. Relatively little is said concerning silviculture broader afield in Europe and almost nothing concerning America or the rest of the world. One realizes that the German silviculturist is apt to be restricted in his knowledge and understanding to what is written in the German language fully as much as the American is usually limited to what is written in English. None the less, the present edition will be valuable in providing the English-speaking forester with an insight into an important and respected silvicultural philosophy as it applies to a region where it was largely evolved.

Squash Technique for Chromosome Studies in Pine Needles and Root Tips of Slash Pine

BY
FRANCOIS MERGEN
HELEN M. NOVOTNY

CHROMOSOME COUNTS in the *Pinaceae* are most easily obtained from female gametophyte cells which have haploid tissue. Many of the trees to be studied are not old enough, however, to produce megasponangiate strobili. In this instance, the best way to obtain squash preparations for counting is to use cells from actively growing root tips or from the bases of young needles. The chromosomes of the pines are very long and have a tendency to become "tangled up" within the dividing somatic cells, making it difficult to obtain accurate counts. Slides for chromosome counts must contain mitotic divisions in which the metaphase chromosomes are well separated and short, and are distributed throughout the cell in one plane. They also should be stained heavily so that they contrast sharply with the cytoplasm. A schedule which has given good results with slash pine tissue is outlined in this paper.

Material and Methods

As part of a study on the induction of polyploidy in slash pine (*Pinus elliottii* Engelm.),[1] several standard squash techniques (Warmke, 1935, and Johansen 1940) were tested on root tips and needle bases. The test material was obtained from freshly germinated seed and from seedlings of up to four months of age. None of these methods tested were found to be satisfactory for counting the chromosomes. Almost all of the dividing cells showed anaphase or telophase figures, and the chromosomes were too long. The needles for study were collected during the morning hours (6, 7, 8 and 9 a.m.) from seedlings growing in a greenhouse. The results indicated that both temperature and light in the greenhouse at the time of collection greatly affected the stages of cell division. Needles collected between 8:00 a.m. and 9:00 a.m., when the temperature and light intensity in the greenhouse was relatively high, had the largest number of figures. Therefore, the plants were brought into a warm room on the afternoon preceding collection to stimulate active cell division. Good results were also obtained when the plants were placed for 45 minutes under a Fluomeric[2] light at an

[1]The polyploidy induction study is made possible through the generous financial support by the West Virginia Paper Company.

[2]"Fluomeric" is a trade name for a high intensity lamp which combines an arc tube with a filament bulb. Optimum range of rendition in visible spectrum: 400-750 millimicrons.

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TABLE 1. Average frequency of chromosome configuration in slash pine cells pre-treated with colchicine. The optimum treatment time (indicated by parentheses) which resulted in the largest number of chromosomes in the metaphase condition decreased as the concentration of colchicine increased.

Treatment	Number of figures			
	Prophase	Metaphase	Anaphase	Telophase
Control	3	0	0	0
1% Colchicine—5 minutes	0	0	0	0
2% Colchicine—5 minutes	15	4	1	1
4% Colchicine—5 minutes	25	(8)	0	9
1% Colchicine—30 minutes	1	0	0	0
2% Colchicine—30 minutes	20	(15)	0	1
4% Colchicine—30 minutes	4	0	1	1
1% Colchicine—60 minutes	26	(44)	0	0
2% Colchicine—60 minutes	13	2	0	0
4% Colchicine—60 minutes	4	0	0	0
1% Colchicine—120 minutes	2	0	0	0
2% Colchicine—120 minutes	0	0	0	0
4% Colchicine—120 minutes	0	0	0	0

intensity of 900 foot candles. To shorten and straighten the chromosomes, and to arrest cell division at the metaphase stage, the needles and root tips were treated immediately after collection, and before fixation, using the following procedures: Soaking in saturated paradichlorobenzene for periods of 1 to 5 hours (Meyer, 1945); soaking in a 3 percent solution of methyl alcohol for 1 to 4 hours (Sass, 1951); chilling in a deep freeze for periods of 1 to 25 minutes (Mehra and Khoshoo, 1956); and treatment with an aqueous solution of colchicine in concentrations of 0.01 percent to 4 percent in full sunlight and under a Fluomeric light for periods of 5 minutes to 2 hours (Bahduri, 1940; Meyer, 1943; Johnson, 1945; McKay and Clarke, 1946; and Mehra and Khoshoo, 1956).

Acetic alcohol (3:5) was used for fixation throughout the experiments and the tissue was macerated in 1N HCl by quick boiling in a test tube or by digestion at 60° C. for 25 minutes. The methods tried for staining the chromosomes included aceto-carmine, propio-carmine, the Feulgen technique, and a new schedule with crystal violet.

Results

There was a slight shortening and straightening of the chromosomes in the tissue which was pre-treated in 3 percent methyl alcohol for 4 hours. However, few cells were evident in the metaphase condition. Neither chilling nor soaking in paradichlorobenzene had any visible effect on the dividing cells. Those cells which had been in the deep freeze for a period longer than 20 minutes had become plasmolized. Treatment with colchicine, on the other hand, prevented spindle formation, and increased the number of metaphase chromosomes. It also shortened them considerably and caused them to be spread throughout the cell. The slides of the needles which were pretreated with colchicine were evaluated and the number of figures in the prophase, metaphase, anaphase, and telophase conditions were counted. In Table 1 are given average values for some of the treatments. Most of the slides, which were prepared during the study of the effect of

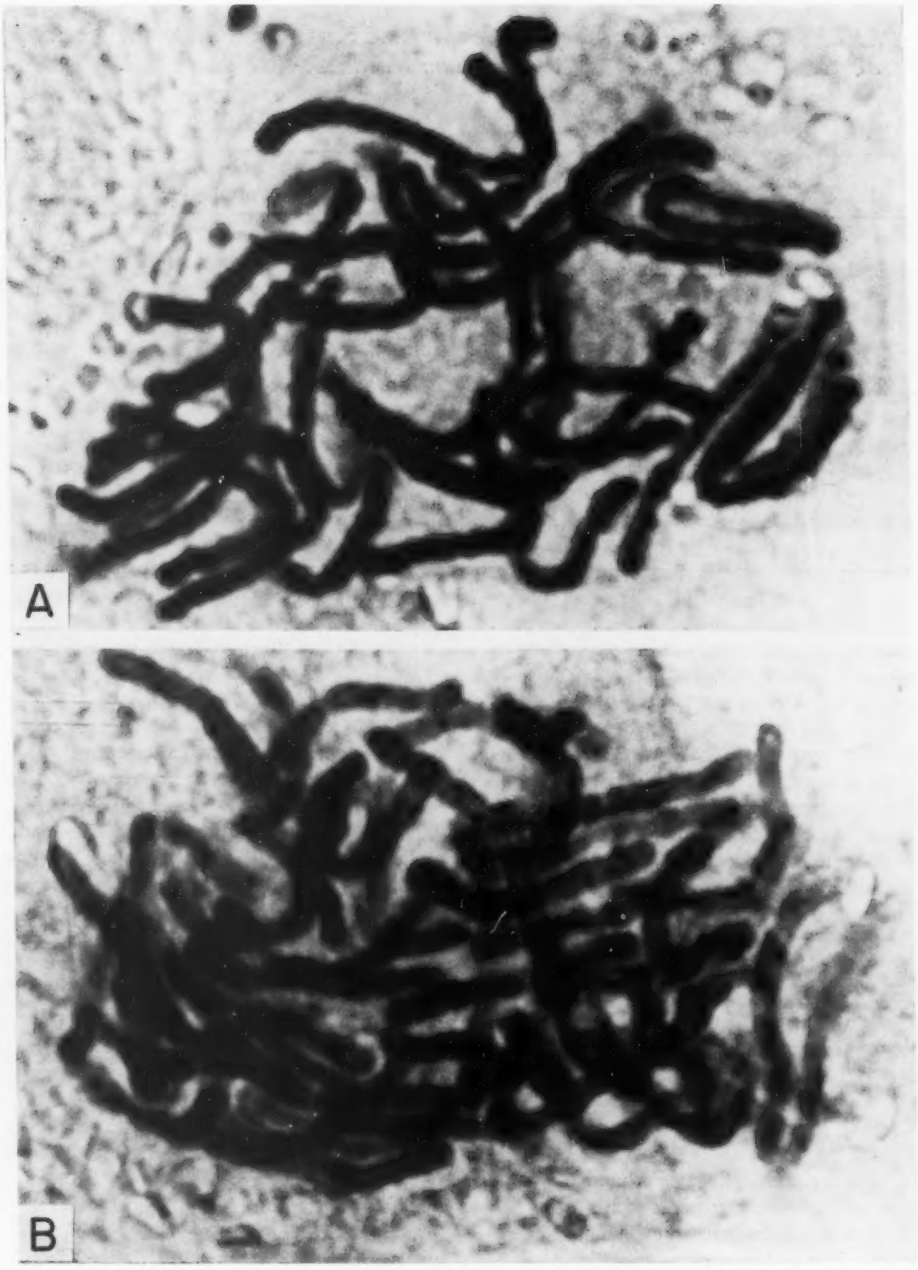

FIGURE 1. *Slash pine chromosomes in the meristematic tissue of the needle. A. A diploid cell ($2n = 24$) showing the chromosomes in metaphase ($\times 2300$). B. Tetraploid cell ($4n = 48$) with the chromosomes in metaphase ($\times 1550$).*

concentration of colchicine and time of treatment, contained actively-dividing cells. Some slides, however, contained only cells with their nuclei in an interphase condition. This was probably the result of plucking needles too far away from the growing points. As can be seen from the values in Table 1, treatment for a 60-minute period in a colchicine concentration of 1 percent resulted in slides with the largest number of metaphase plates. A higher concentration, or a longer treatment period was less favorable. A lower light intensity also gave poorer results.

Of the stains tested, crystal violet was most specific for the chromosomes, and brought about the clearest contrast with the cytoplasm. This was especially pronounced when counterstained with fast green. For immediate examination, the macerated and stained cells were mounted in distilled water and the cover glass ringed with paraffin. However, more permanent slides were obtained by mounting in clear Karo corn syrup. Of a series of over 100 permanent slides made by this last method, all showed chromosome plates which could be counted, including those in 2n, 3n, 4n, and 8n cells (Figures 1A and 1B).

Schedule

Following is the schedule which gave best results:

1. Soak freshly collected needles or root tips for 60 minutes in a 1% aqueous colchicine solution in bright sunlight, or place under an artificial light (Fluomeric) of 900 foot candles.
2. Fix in acetic alcohol (3:5) for 24 hours at room temperature, or for 30 minutes at a temperature of 60° C.
3. Rinse in 1N HCl, and hydrolize in fresh 1N HCl for 25 minutes at a temperature of 60° C.
4. Stain in crystal violet for 10 minutes (1 g. of crystal violet in 100 cc of 50% ethyl alcohol).
5. Destain in 70% ethyl alcohol—15 seconds for needles and 30 seconds for root tips.
6. Step down to distilled water in rapid steps — 30 seconds in 50%, 30%, and 15% alcohol.
7. With a sharp razor blade, cut off meristematic tissue at base of needle or at tip of root (1 mm to 5 mm) and (*a*) place in drop of distilled water on slide, or (*b*) place in a drop of fast green prepared by adding 10 drops of a saturated alcoholic solution of fast green to 10 cc of distilled water.
8. Cover with a No. 1 cover glass and apply presure over the material to separate the cells.
9. Place in a bibulous book and apply pressure to remove as much water as possible.
10. (a) Ring with paraffin and examine
    or
    (b) Gently raise cover slip with razor blade and place a drop of white Karo syrup on slide. Replace cover glass in the same position and press out the excess Karo, which may then be washed away with water.

Note: A good way to dry the slides is to leave them overnight with a small lead weight on the cover glass. Protect cover slip by placing soft paper between weight and slide.

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Growth Habits of the Eucalypts

By M. R. Jacobs. Forestry and Timber Bureau, Commonwealth of Australia. Canberra. 262 pp. 1955.

Review by John W. Duffield
Col. W. B. Greeley Forest Nursery, Nisqually, Washington

The title of this work may hide its general silvical and silvicultural interest. This is an extremely meaty and thought-provoking piece of work, and should prove of value to forest biologists who have never seen and never hope to see a eucalypt.

The 630-odd species of *Eucalyptus* cover a climatic range in Australasia which includes at its extremes the deserts of interior Australia, the alpine forests of Tasmania and southeastern mainland Australia, and the tropical rain forests of northeastern Australia, New Guinea and the southern Philippines. Over this range, particularly in its temperate portions, there is scarcely an ecological niche without its eucalypt, and in many of these niches, the eucalypts are making important contributions to the economy of the area. In addition, the genus has furnished useful wood-producers to many of the warmer regions of the world. For these reasons, this study of a single genus has much wider implications than would appear at first thought.

Selected topics from the table of contents may give some idea of the scope of this work. These are: the four ways of producing leaves, the life of the leaves, the shedding of the branches, general branch habit, growth stresses (this is material not dealt with elsewhere in the literature of forestry or botany), phenomena associated with a gap in the forest, crown shyness and abrasion, verticality, features of the root system, the importance of bark. In addition, there is a 60-page section on the effect of growth habits on the treatment of Australian eucalypt forests, which amounts to a thorough systematic review of eucalypt silviculture.

This book brings together much of the excellent material published in the bulletins of the Forestry and Timber Bureau, many of which are out of print and not readily available to foresters outside of Australia. Jacobs has been the author of many of these, and the present work includes, in addition, a great deal of original work resulting from field exercises of the Australian Forestry School, of which Jacobs is Principal and Lecturer in Silviculture.

From a pedagogue's viewpoint, there is only one rather questionable section, namely that dealing with branch orders, in which the role of auxins seems to be slighted for a less plausible explanation. Selected portions of this book should be invaluable as supplementary readings in courses in silvics and silviculture, particularly at those points at which the modern instructor reluctantly refers to the now dated Büsgen and Münch. If the reviewer were teaching, he would want to have several copies of Jacobs in the school library.

Seasonal Height Growth of Conifers

BY
THEODORE T. KOZLOWSKI
RICHARD C. WARD

REMARKABLE DIFFERENCES exist in seasonal height growth patterns of different species of trees. Species differ markedly in total amounts of seasonal height growth and in the lengths of their growing seasons. Although height growth is determined by interactions of hereditary potentialities and environmental factors, the length of the growing season and the shape of the growth curve of a species are apparently controlled most by hereditary factors and appear to be relatively independent of normal fluctuations in environmental factors. Severe droughts or excessively low temperatures may check height growth somewhat but the usual variations in moisture and temperature apparently have little effect (Kramer, 1943). Kramer compared Kienholz's growth curves for white and red pine in New Hampshire with his own data for the same species in North Carolina. He found that the severe change in environment that resulted from transferring white and red pine from New England to North Carolina merely increased somewhat the absolute lengths of their growing seasons but did not change the relative lengths or shapes of their growth curves. The impress of hereditary control on seasonal height growth of conifers has also been stressed in several other studies in different regions (Baldwin, 1931; Kienholz, 1934, 1941; Huberman, 1940; Cook, 1941a, 1941b; Fowells, 1941; Johnston, 1941; Friesner, 1942, 1943).

The present study was initiated to extend work done on older trees to seedling conifers to see whether the marked variations in height growth between species observed in older trees in plantations and forests would manifest themselves in a managed forest nursery in soil of high fertility and known physical characteristics. Other objectives were to obtain additional height growth data for central Massachusetts for comparison with data from other regions and to make comparisons of growth patterns of seedlings with those of older trees of the same species.

Methods

Five species of three-year-old coniferous seedlings under regular nursery management at the State Forest Nursery, Amherst, Massachusetts, were used. The soil was Melrose fine sandy loam with a moisture equivalent of 16.16 percent and a permanent wilting percentage of 5.52. The species used were white spruce (*Picea glauca* Moench), Norway spruce (*Picea Abies* (L.) Karst.), eastern hemlock

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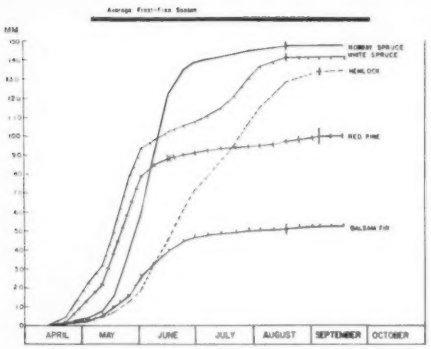

FIGURE 1. *Total height growth of 5 species of conifers during 1954 at Amherst, Mass.*

(*Tsuga canadensis* (L.) Carr.), red pine (*Pinus resinosa* Ait.), and balsam fir (*Abies balsamea* (L.) Mill.). In the spring of 1954 twelve seedlings of each species were marked and measured for height growth beginning in early April. A branch near the tip was selected and marked as a base from which to make measurements to the tip of the leader. Measurements of height growth were made at approximately weekly intervals throughout the growing season of 1954.

Results

The total amount of height growth throughout the growing season of 1954 is given in Figure 1. Buds began to swell between April 12th and 21st, with the average initiation date for different species varying from April 15th to April 20th. White spruce and red pine made a rapid start, while balsam fir and hemlock lagged behind. Norway spruce was intermediate but soon outgrew all the other species. It had the highest growth rate of all between June 1st and 8th, 4.6 mm for a day and reached maximum height. Hemlock started slowly but caught up with and surpassed red pine by June 19th, while red pine had slowed down by that time, and its growth was thereafter limited to bud elongation.

Figure 2 shows cumulative percentages of total seasonal growth that had been completed at various dates during the growing season. The rapid increase in growth of red pine and white spruce as well as the lag in growth of hemlock are clearly evident. A pattern of deceleration of growth in June followed by an acceleration late in July is shown by only one species, white spruce. Table 1 summarizes additional pertinent growth data.

Figure 3 shows the percentage of the season's height growth which was added during each month. May was the month of greatest growth for red pine and white spruce while Norway spruce, balsam fir, and hemlock made more growth in June than in any other month. Balsam fir, however, grew almost as much in May as in June. White spruce had a maximum increment in May, a deceleration of growth in June, and a second but weaker growth burst in July. Hemlock grew conspicuously more in July and August than the other four conifers and continued to grow into September.

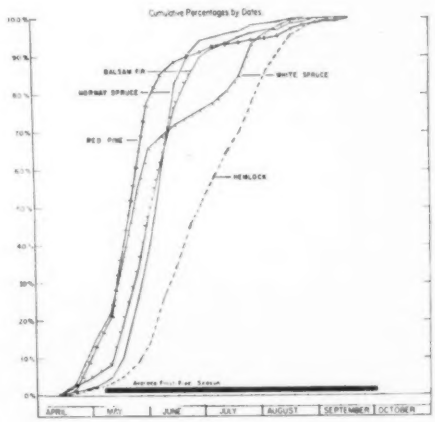

FIGURE 2. *Course of seasonal growth of 5 species of conifers during 1954 at Amherst, Mass. Growth plotted as per cent of season's total completed at various dates.*

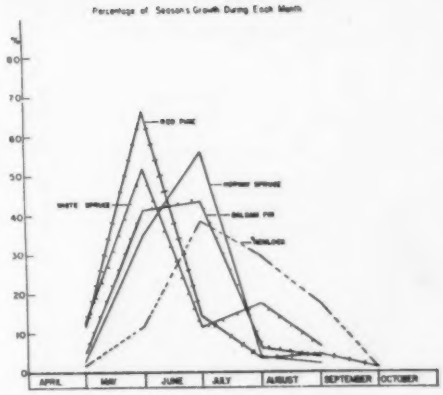

FIGURE 3. *Percentage of season's height growth added during each month for 5 species of conifers during 1954 at Amherst, Mass.*

Discussion

The present study reemphasizes the importance of hereditary control over height growth patterns of trees. Each species manifested individuality of seasonal growth pattern despite the fact that all the seedlings were grown in soil of high fertility and the relatively similar environment of a managed forest nursery. Marked species differences were shown in total amount of growth as well as in length of growing season.

All species started growth before the threat of frost was over and completed all growth during only a part of the frost-free season. The average date of the last frost of spring in Amherst, Massachusetts is May 7th while the average date of the first frost in autumn is October 2nd. Ninety-five percent of the growth of all five species was completed by mid-August (Table 1). In fact one species, Norway spruce, had completed 95 percent of its growth as early as July 7th. In an average frost-free season of 148 days for Amherst all species had completed the middle 90 percent of their seasonal height growth in 57 to 103 days.

The growth curve for red pine in the present study is very similar in shape to the growth curve of red pine in North Carolina and of red pine in New Hampshire (Compare Fig. 3 with Fig. 4 of Kramer, 1943). However, in North Carolina the peak occurred in April; in Massachusetts in May; and in New Hampshire in June. The similarity in growth patterns of the three-year-old trees of the present study with Kienholz's (1934) nine-year-old trees emphasizes that in many respects seedlings of this species behave like older but not necessarily mature trees. Wareing (1956) stated that in many woody species the seasonal period of height growth is much shorter in mature trees than in

TABLE 1. Growth data for three-year-old conifer seedlings at Amherst, Massachusetts, during the growing season of 1954.

Species	Norway spruce	White spruce	Red pine	Balsam fir	Eastern hemlock
Average original height, cm.	36.0	10.5	18.0	15.0	15.0
Average increment, mm.	148	142	100	52	134
% increase	41	135	56	35	89
Date growth started	Apr. 15	Apr. 20	Apr. 20	Apr. 15	Apr. 15
Date growth stopped	Aug. 18	Aug. 18	Sept. 5	Aug. 18	Sept. 5
Duration of growth, weeks	18	18	20	18	20
Date 5% growth completed	May 11	Apr. 23	Apr. 25	Apr. 30	May 16
Date 95% growth completed	July 7	Aug. 1	Aug. 6	July 21	Aug. 17
Days required to complete 90% of growth	57	99	103	82	93

seedlings. For example, seedlings of *Robinia pseudoacacia* had a long growing season which extended into the autumn, but in mature trees of this species tip growth of many shoots ceased by the end of July. Wareing postulated that in older trees such factors as competition between various shoots for nutrients may be more important than in seedlings. Hence he cautioned against arriving at conclusions about growth of mature trees by extrapolation from the periodic behavior of seedlings. On the other hand, Cook's (1941b) 8-year-old hemlocks had a very long growing season as did the much younger hemlocks of the present study. In another study, Cook (1941a) did not give tree ages but did give tree heights and pointed out that the conifers he studied were well established plantation trees. Height growth of his 7-foot red pines was similar to that of the much younger trees of the present study and to Kienholz's 9-year-old trees to the extent that in all three studies this species completed most of its growth early in the year. The two- or three-year-old seedlings of loblolly pine studied by Kramer (1943) in Durham, North Carolina started growth about the same time as the 13-year-old loblolly pines of Young and Kramer (1952), but they grew somewhat later in the autumn. Nevertheless there was considerable similarity in the growth patterns of the young seedlings and the 13-year-old trees.

These comparisons not only stress the importance of species differences and hereditary control of height growth, but suggest further that in some species the seasonal height growth pattern may be similar over a considerable age span. Seedling data for some species may be more reliable than for others as an index of physiological response of more mature trees. Data which critically establish the extent to which seedling response may be extrapolated to older trees are certainly not voluminous and more are needed. Further generalizations may be anticipated when much more necessary phenological data are accumulated for trees of varying age. Nevertheless most of the processes of large trees, except flowering and fruiting, can be observed in seedlings as well as in mature trees and many basic species differences in response may be demonstrated with tree seedlings (Kramer, 1943; Kozlowski, 1955). Furthermore, work with tree seedlings should be encouraged because in many studies of competition and succession the responses of seedlings and young trees are often of greater importance and interest than responses of mature trees.

There appears to be little correlation between total amount of growth and length of the period during which it occurs (Figs. 1 and 3; Table 1). The average growth period of balsam fir, which grew least, was the same as that of white and Norway spruce. Eastern hemlock and red pine grew over a longer period than the other three species, but the total amount of growth was intermediate.

Current-year height growth of deciduous trees with short growing seasons may be made mostly at the expense of prior-year photosynthate (Loomis, 1935). Possibly trees with longer growing seasons use not only reserve foods from the previous year but also products of current photosynthesis (Kozlowski and Ward, 1957). The present study suggests there may be some basic differences in conifers with regard to degree of dependency on prior-year and current-year photosynthate. The rapid start of white spruce suggests great dependency on carbohydrate manufactured during the prior year. Recently Ferchau (personal communication, 1956) observed that apparent photosynthesis of hemlock seedlings was intrinsically low, and this suggests that hemlock does not accumulate large carbohydrate reserves. The lack of a pronounced growth surge in spring may reflect a low amount of accumulated food. Its slow start and its long continuation of growth in the late summer suggest that hemlock depends on current-year photo-

synthate for height growth during much of the growing season. Further experiments on species like white spruce and hemlock are needed to determine the amounts of carbohydrate they store and use at various times of the year. More research on food accumulation and subsequent utilization is needed for trees with long and those with short growing seasons. Such information may be helpful in enhancing knowledge of tree growth.

The authors acknowledge the cooperation of Mr. Charles Palmer, Superintendent of the State Forest Nursery, Amherst Massachusetts, whose courtesy made this study possible.

Summary

1. Three-year-old seedlings of five species of conifers were measured in the State Forest Nursery in Amherst, Massachusetts for height growth at approximately weekly intervals during the growing season of 1954.

2. Red pine and white spruce made the most rapid initial growth, but red pine formed buds in mid-June and subsequent growth was only bud elongation. White spruce slowed down in early June and had a second burst of growth in mid and late July. Norway spruce started slowly but soon outgrew all other species. Balsam fir grew least.

3. Balsam fir and hemlock started growth slowly. Balsam fir soon reached a maximum and then slowed down while hemlock kept on growing at a slowly diminishing rate from early June to mid-August.

4. No relationship was found between the length of the growing season and the amount of growth in any species.

5. Comparisons of data for young seedlings and older trees show that, in some species at least, growth patterns are similar over a considerable age span.

6. All trees started growth in the spring before danger of frost was over and stopped growing in the summer usually long before fall frosts began.

7. Differences in growth patterns of white spruce and hemlock suggest that in hemlock more current-year photosynthate is utilized in height growth.

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Recording Micrometer

Machine for measuring annual rings. Ab Addo, Malmö, Sweden (U. S. agent, Addo Machine Company, Inc. 145 West 57th St., New York 19.) $3,000.00.

Equipment Note by Stephen H. Spurr
Professor of Silviculture, University of Michigan, Ann Arbor

The Swedish tree-ring micrometer has considerable value for both research and major forest inventory use. It consists essentially of a binocular microscope mounted over a long stage, the movement of which is tied in to an adding machine converted to record the amount of movement of the stage. The stage is especially constructed to hold an increment core, and an attachment is provided on which a tree cross-section can be mounted. In use, the increment core or other object is cranked past the image of a cross-hair in the microscope eyepiece, and the distance traversed may be recorded at any point by touching the add bar on the adding machine. Various gear combinations permit the recording of distance travelled to the nearest 0.1, 0.2, or 0.01 mm.

The instrument was developed by the Swedish Forest Research Institute for the handling of large numbers of increment cores mailed to a single central office in the course of the national inventories of Sweden's forests. Since the first model was constructed in 1930, a series of improvements and refinements have been added until the present model is exceedingly well designed. The details of its design and its use in Sweden are incorporated in an article written in Swedish, but the figures and tables have English subtitles and the article includes a detailed English summary.[1]

The instrument is used for two different types of analysis: (1) Determining the diameter inside bark for each of the past five years; and, in addition, the age of the tree; and (2) Determining the width of the last 12 annual rings in studies of ring growth,

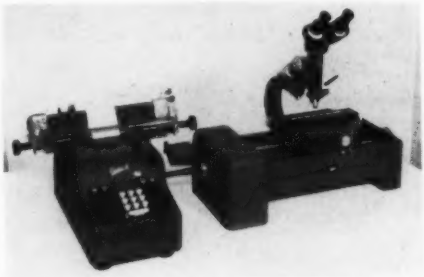

FIGURE 1. *The Swedish recording micrometer for use in wood growth studies.*

including studies of the effects of climatic fluctuations. The measurements are recorded by the adding machine directly on to standard forms. Analysis of the data is accomplished through business machine cards.

Although the instrument is designed particularly for the measurement of tree rings, it can be used wherever precise measurements need to be taken from a longer specimen than can be accommodated in the ordinary microscope stage. It can readily be used in measuring such items as crown diameters on aerial photographs, vessel widths on photomicrographs, fish scales, and similar measurements of insects. In the Department of Forestry at the University of Michigan, it is being used particularly on studies of (1) wood-growth relations and (2) the effect of climatic fluctuations on growth in forest trees.

As of early 1957, nine such machines were in use in Sweden, three in western Germany, and one each in Finland, Japan, Norway, Switzerland, Turkey, U.S.A., and eastern Germany. At least one additional instrument has since been purchased for use in this country.

[1]Eklund, Bo. 1947. (The Swedish Forest Research Institute's machines for measuring annual rings.) Medd. f. Statens skogsförsöksanstalt 38 (5): 1-77.

Effects of Water Upon the Seed Germination of Bottomland Trees

BY
JOHN F. HOSNER

A NUMBER OF STUDIES dealing with the ecology of bottomland hardwood trees have emphasized the selective effect of flooding upon regeneration. No attempt, however, has been made to determine the relative tolerance to water of the seeds of various bottomland species. The following study was set up to determine the effects of water upon the seed germniation of red maple (*Acer rubrum* var. *drummondii* Hook and Arn.), silver maple (*Acer saccharinum* L.), American elm (*Ulmus americana* L.), sycamore (*Platanus occidentalis* L.) and eastern cottonwood (*Populus deltoides* Bartr.).

A number of authors have pointed out the effect of inundation of tree seeds. According to Baker (1950) seeds soaked in water will swell and the seed coat may crack, but unless removed, the seed will then decay. Lack of oxygen apparently is the limiting factor. Low oxygen tensions have been demonstrated to limit the germination of pinon-pine (Baker, 1950) and aspen (Faust, 1936). In bottomland hardwoods it seems that oxygen may be inadequate when the seed is in water or between matted, sodden leaves or buried too deeply in poorly aerated soil. Putnam (1951), in evaluating the water effect, stated that "no seeds can germinate under water" and "a copious seed supply (in wet areas) is essential to offset the hazards of submergence."

Baker (1950), in summarizing the work of Toumey and Durland (1923), pointed out that some seeds are far more tolerant of oxygen deficiency than others. He reported that seeds of most upland species were seriously injured by soaking in water for more than 10 days and that a deleterious effect began to be evident after about 3 to 5 days. Demaree (1932) reported that cypress seeds have been kept in water as long as 30 months without injury. Barclay (1924) stated that cottonwood seed will sink in water and remain viable from the latter part of May to September.

Thus, is seems to be a well-accepted fact that tree seeds, after prolonged water coverage, show different responses to germination, but the relative tolerances of the various bottomland species have not been measured.

Procedure

Samples of 100 fully developed and apparently sound seed of red maple, silver maple, American elm, sycamore and eastern cottonwood were randomly selected from seed collected during the 1956 spring seeding period for each species. The samples were then randomly split into two lots of 50 seeds each. One lot of each sample

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TABLE 1. Initial germination and germination after storage of four species of bottomland hardwoods.

Treatment period	Mean number of germinating seed per lot of fifty seeds[1]			
	Red maple	Silver maple	Sycamore	Elm
0 unsoaked	47.7	49.7	16.0	15.7
4 soaked	49.7	49.7	18.0	29.7
unsoaked	47.7	48.3	9.3	21.7
8 soaked	48.0	49.0	28.3	42.7
unsoaked	48.0	47.7	27.3	37.7
16 soaked	45.7	49.3	24.3	42.7
unsoaked	47.3	49.0	25.3	30.7
32 soaked	46.7	49.0	25.0	30.3
unsoaked	44.3	41.0	18.3	28.3

[1]The numbers shown are means of three replications.

was placed in quart mason jars filled with tapwater, and the other lot was placed in an empty air dry jar. Both containers were covered and kept in a darkened root cellar with a relatively constant temperature of about 60°F. The treatment periods were 4, 8, 16 and 32 days. Each treatment was replicated three times making a total of 150 seeds per species treatment.

As a check on initial germination three lots of fifty seeds each were tested for germination at the time the treatments were started.

Upon the completion of the appropriate treatment period each lot of seeds was removed from the root cellar and planted in compressed sphagnum moss germinating beds as described by the U. S. Dept. Agric. (1948). The germination tests were continued until no new germination occurred over 5 day periods.

Results

Except for sixteen red maple and two silver maple seeds, which had protruding radicals, the seeds of elm, sycamore, red and silver maple did not germinate during the soaking period in the water. The seeds of sycamore and elm sank after a few days of soaking. Those of silver and red maple varied with approximately one-half sinking and the rest floating. Upon removal from the water, however, germination at room temperatures was consistently good regardless of the soaking period or whether the seeds floated or sank. The seeds with extended radicals continued to complete germination. The mean number of germinating seeds for each species and treatment is shown in Table 1.

The table indicates that soaking in water up to 32 days does not inhibit the seed germination of these species. In fact, quite the opposite was true with some species. The soaked seeds of elm had a consistently higher germination than the unsoaked seeds for all treatment periods. For the other species there were no consistent trends although at the 32 day period the soaked seeds of all species germinated better than the unsoaked seeds. Apparently, storing dry seeds for 32 days at a temperature of 60°F. results in some viability loss.

The results of soaking the cottonwood seeds were quite different. Approximately half the seeds floated and half the seeds sank in the water. After four days of soaking apparently all the viable seed had germinated in the water regardless of whether they were floating on the surface of the water or resting on the bottom of the container. Also, the water did not seem to slow the rate of germination. Upon removal from water no additional germination was obtained from the cottonwood seed.

Subsequent field observations verified these laboratory findings. Cottonwood seed was observed in shallow pools of water in the bottomlands of southern Illinois. Some of the seed floated on the surface of the water while others sank. In either case much of the seed germinated. Those germinating on bottom of the pools appeared erect and normal in all respects.

Checks with limited amounts of black willow (*Salix nigra* Marsh.) indicated that black willow germinated similar to cottonwood. Most of the seed sinks in water and germinates immediately. No loss in germinability was evidenced by the unsoaked but stored seed of cottonwood and willow up to 16 days, but at the end of 32 days only one cottonwood seed and none of the willow seeds germinated.

Discussion

Many factors such as temperature, amount of water movement, chemicals and organic matter in water, microbes, algae growth and the like, would be expected to affect the length of time that seeds and seedlings will tolerate soaking, but it does not seem likely that natural flooding is a major factor causing selective regeneration in the wetter bottomland forests, except possibly in swampy areas and areas where water is ponded for more than a month during the grownig season. In fact quite the opposite seems true; that is, flooding at least for short periods seems beneficial. Rarely do floods last more than 32 days.[2] Then too, the seeding period extends for at least two weeks for all the species mentioned and longer for sycamore, cottonwood, and willow, making it unlikely that flooding would cause an appreciable loss in a season's seedcrop in the area studied. Also, in view of the immediate germination of cottonwood seeds in water, Barclay's (1924) observations concerning cotonwood seeds remaining viable in water over the summer period do not agree with the conditions and results in this study. Observations in southern Illinois indicate that it is not uncommon for cottonwood trees to be maturing viable seed in mid-August. Thus, a more plausible explanation would be that what she considered seed inundated over the summer period was newly cast seed in late summer that was presumed to have been distributed during the spring.

In view of the above results, it would seem that the commonly reported effects of floods upon the regeneration of bottomland species are much more apt to be the result of heavy deposits of silt accompanying floodwaters or to be the effects of water upon the germinated seedlings rather than due to the inhibiting effects of the water on seed germination as such.

Summary and Conclusion

Seeds of six species of bottomland hardwood trees were subjected to soaking in tapwater in a darkened root cellar at approximately 60°F. for periods varying from 4 to 32 days. Generally, red maple, silver maple, sycamore, and elm seeds failed to germinate while soaking in water but immediately upon removal germination was rapid and consistently high for all periods of time. For similar periods the soaked seeds of sycamore and elm tended to have higher germination than the unsoaked check seeds.

Cottonwood and willow seeds completed their germination in the water in four days of soaking. Many seedlings of both willow and cottonwood removed from the water after 32 days appeared as healthy and normal in all respects as seedlings germinated in sphagnum moss germinating beds from unsoaked seeds.

It was concluded that, except possibly through indirect effects of siltation, flooding of bottomland hardwoods up to periods of 32 days does not seem to have an appreciable effect upon the germination of the six species tested.

[2]Fifteen year records taken by the State Water Survey at New Athens, Illinois along the Kaskaskia River showed that the average consecutive period that the river was out of its banks was 20 days.

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The Future of Arid Lands

Edited by Gilbert F. White. 453 pp., illus. American Association for the Advancement of Science, 1515 Massachusetts Ave., Washington 5, D. C. 1956. $6.75 ($5.75 to AAAS Members).

Review by Stanley A. Cain
Charles Lathrop Pack Professor of Conservation
University of Michigan, Ann Arbor.

This volume consists of papers from the International Arid Lands Meetings, New Mexico, April 26-May 5, 1955, sponsored jointly by the AAAS, the National Science Foundation, the Rockefeller Foundation, and UNESCO. The papers by scientists from 17 countries are twice that in number and are grouped in the following broad categories: the broad view, variability and predictability of water supply, better uses of present resources, prospects for additional water sources, and better adaptation of plants and animals to arid conditions.

Many of the authors centered their attention on areas of needed investigation and improvement of understanding of data. Tremendous gaps in knowledge were uncovered and profitable lines of research were pointed out. Participants covered a wide range of technical fields, such as agronomy, soils, forestry, hydrology, climatology, geology, genetics, physiology, ecology, geography, conservation, economics, archeology, cultural anthropology, botany and zoology. As Professor White pointed out in the Preface, "when many disciplines join in viewing an old problem the traditional perspectives are challenged. . . " Data and experience were drawn from North, Central and South America, North Africa and the Mediterranean, the Middle East, and other dryland areas.

Although grazing and types of arid farming received most attention in the land-use field, forestry was not ignored. For example, R. O. Whyte, Plant Production Branch of FAO, points out that the forester has an important although specialized role to play in arid and semi-arid regions. His role is not only in planting of fuel lots, shelter belts and fodder trees; it lies also in regeneration of scrub vegetation and woodlands, systems of protection, and the development of new products from native and adaptive woody species. Use pressures are generally high in arid lands despite the low carrying capacity and both human and animal populations often are far above safe limits.

Although this book has relatively little of direct interest to humidland foresters, the papers are interesting, thought-provoking and, I believe, useful for foresters and land-use scientists generally. There is much here that has general meaning.

Double Branch Whorls in White Pine

BY
BENSON H. PAUL

A STUDY of the development and persistence of knots in white pine revealed a double set of branch whorls at each node in plantation-growth white pine in North Carolina. There was no satisfactory explanation of the cause of this excessive branching. Similar multiple branching was observed on other young white pine trees in the vicinity. In some instances, there were as many as 20 branches at what appeared to be the same node.

In tree improvement programs, it would be of interest to know whether or not this branching characteristic is hereditary or if it can be attributed to certain climatic conditions of the locality.

Upon examination of the interior of the trees in which double branching occurred, it appeared that following the usual elongation of the stem and the formation of a terminal and lateral buds, a second elongation took place in the same growing season along with the development of a new terminal and another set of accompanying lateral buds. The extent of the secondary elongation sometimes was less than 1 inch. Figure 1 shows the initial development of two branches, one above the other, and the points of their beginnings at the pith of the

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FIGURE 1. *The initial development of 2 branches, 1 above the other, and the points of their beginnings at the pith of white pine.*

FIGURE 2. *Numerous branches at the nodes in plantation-grown white pine in North Carolina.*

tree. Figure 2 shows numerous branches at the branch nodes in the trees.

If growth of this kind is hereditary, seeds of such trees would be undesirable for planting, since lumber from such trees would have twice as many knots if left unpruned. If pruned, the pruning costs would be greater because of the extra work necessary in the pruning operation.

A Logical Approach to Isolation Strip Width

BY
EDWARD G. ROBERTS

THE EXPERIMENTER frequently sets such narrow limits on conditions to be tested that these limits can be met only on small areas. With suitable area restricted, he reduces plot size to that which he considers to be the minimum and then surrounds it with an isolation strip. Apparently no guides to minimal isolation strip widths have been established through logical reasoning. The only guide known to the writer is that the isolation strip should be as wide as the trees are (or will become) high. The reasoning behind this recommendation is obscure. In desperation, perhaps, workers often surround a plot with a chain-wide isolation strip, put a quarter-acre plot in the middle of an acre, or employ some other arbitrary mathematical scheme.

A plot must be isolated from a surrounding area which may, through its different nature, impinge unlike conditions of root competition, side light, or wind on the trees of the plot. In many cases, the conditions of the adjacent area would be sufficiently like those on the plot so that side light and wind would differ little if at all. Some examples where this would be so are in plots where intermediate cuttings are being tested (as in thinning to different basal areas) and in comparisons within a reproduction method (as with plots managed selectively but with different growing stock volumes). On the other hand, side light and wind conditions would vary widely where, for example, a clearcut plot adjoined one which was cut selectively. Certainly in many cases, however, the most important condition from which the plot should be isolated seems to be differences in root competition.

The roots of a tree surrounded by the root systems of other trees and in competition with them will radiate outward in a circular manner, yet they cannot, on the average, occupy a circular area. Adjacent circles will not fit together. It is, likewise, unreasonable to expect the roots of such a tree to occupy a rectangular area. Indeed, the most reasonable assumption is that, on the average, the roots will occupy a hexagonal area.

This approach to isolation strip width is based, then, on the following assumptions:

1. In many cases, the chief factor from which a plot must be isolated is unlike conditions of root competition.
2. Competing root systems will occupy, on the average, hexagonal areas.
3. On a given site with a given species the land occupied by a tree is directly proportional to its basal area. (On this more later.)

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Example 1

Suppose that plots are being established in a small pole stand for some purpose such as thinning and that it is intended for these plots to be maintained until the trees are sawlog size. At maturity there will be, for simple example, 100 trees per acre. Some trees, by chance, may straddle the plot boundary. At the end of the rotation, such a plot-boundary tree should have the opportunity of being opposed by a like tree on the isolation strip. In this 100-tree-per-acre stand, the distance from the bole of a plot-boundary tree to one opposing it on the isolation strip would be:

$$D = \sqrt{\frac{A}{0.866}} = \sqrt{\frac{435.6}{0.866}} = 22.4 \text{ ft.}$$

where D is the distance between boles (or diameter of a hexagon) and A is the area occupied by one tree. If this isolation strip tree is opposed by a similar one on the isolation strip of the adjacent plot (or has the opportunity to be so opposed), the line between isolation strips would be halfway between the two boles—11.2 ft. The isolation strip width, then, would be 22.4 ft. plus 11.2 ft. or 33.6 ft.

Example 2

The previous calculation is based on the assumption that all 100 trees have the same basal area and occupy equal land areas—an obviously absurd assumption. It should be possible to estimate, with reasonable accuracy, the tree of future maximum basal area and, assuming a direct proportion between basal area and land occupied, the land which such a tree will occupy. This area would be substituted in the formula given in Example 1. Using the previous example, suppose the 100 trees per acre will have a basal area of 120 sq. ft. or 1.2 sq. ft. per tree. The diameter of the tree of mean basal area will be 14.8 inches. On the basis of experience, you estimate that diameters will range from 7 inches to 22 inches. The basal area of a 22 inch tree is 2.64 sq. ft. By simple proportion, the roots of a 22-inch tree will occupy 958.3 sq. ft.

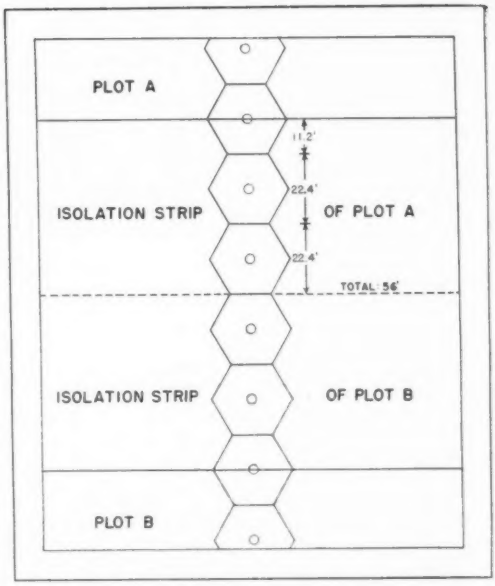

FIGURE 1. *Plot-boundary trees opposed by two like trees on isolation strips.*

Substituting in the original formula, the distance between the bole of such a tree on the plot line and that of a like tree on the isolation strip is 33.2 ft. This distance plus half the distance between the isolation-strip tree bole and that of a tree opposing it on the adjacent isolation strip makes an isolation strip width of 49.8 ft.

Example 3

Where treatments of adjacent plots are quite dissimilar, an isolation-strip tree may have little probability of being opposed by a similar tree on the adjacent isolation strip. It may therefore, be abnormally vigorous and, as a consequence, unduly retard the plot-boundary tree. Where this is felt to be the case, isolation strip width can be provided which will offer the opportunity for the plot-boundary tree to be opposed by two isolation-strip trees. In the first example, this would have provided an isolation strip width of 56 ft. (see Fig. 1) and in the second example 83 feet.

Association of Cytophoma pruinosa with Dying Ash

BY
S. B. SILVERBORG
R. W. BRANDT

WHITE ASH, *Fraxinus americana* L., has been dying in increasing numbers in New York State and other parts of the Northeast during the past 15 years from an unknown disease commonly called ash dieback. Early symptoms of the disease were first observed on roadside and hedgerow trees, but in recent years they have been observed frequently on ash in forest stands. White ash is a valuable timber tree in the Northeast and reduction in its supply is of great concern to the wood-using industry.

While the results of this study are not wholly conclusive at this time, the purpose of this paper is to present data accumulated to date as an aid to other investigators who may be studying this disease.

A study of the disease was begun in 1954. Isolations of fungi from a number of dead and dying ash trees were made in 1954 and 1955 to determine the cause of the malady. *Cytophoma pruinosa* (Fries) Höhn., [*Dendrophoma pruinosa* (Fries) Sacc., *Cytospora pruinosa* (Fries) Defago] was isolated consistently from diseased trees.[1]

The genus *Cytophoma* is distinguished from *Cytospora*, according to von Höhnel (1914), by the non-loculate pycnidia and branched conidiophores of the former. Defago (1942), however, regards the fungus as a *Cytospora*, thus giving it the name of *Cytospora pruinosa*. Several species of *Cytospora* have been reported on *Fraxinus* from North America and Europe. Among them are *C. annularis* Ell. & Ev., *C. minuta* Thüm., and *C. melasperma* Fries var. *fraxini* Allesch. (*C. ceratophora* Sacc. of Fungi Columb. 363). They are all regarded by von Höhnel (1928) as synonyms of *Cytophoma pruinosa*. In 1934 Reddy, *et al.* (1934) found *Cytospora annularis*, one of the synonyms of *Cytophoma pruinosa*, to be the most common fungus species on diseased ash twigs and branches in Iowa. They found that inoculations of this fungus in wounded one-year old white ash trees caused pronounced sunken cankers around the wounds. The fungus killed the tissue beyond the wound, and in many instances almost girdled the trees.

Symptoms of ash dieback

The disease is found on white ash of all age classes from young sapling size to trees 18 to 24 inches d.b.h. The first symptoms appear during the spring or early summer as few to many dead branches, usually in the upper part of the crown (Fig. 1). In

[1]Identification of the fungus was made by Miss Edith Cash, Associate Mycologist, U. S. D. A., Beltsville, Maryland.

Respectively Research Associate and Research Fellow in Botany and Forest Pathology, State University College of Forestry at Syracuse University.

FIGURE 1. *Fifteen-year-old white ash roadside tree, 3 years after the first appearance of dieback symptoms, showing dead branches in the upper portion of the crown and only a relatively few live branches lower in the crown.*

succeeding years larger branches lower in the crown succumb until the entire tree is dead. Small trees approximately 2 to 6 inches d.b.h. are often killed in 2 to 3 years, while larger trees may persist for 5 to 8 years or more.

Definite yellowish to reddish-brown cankers, often slightly sunken and with more or less irregular raised margins, may occur on many of the dying stems and branches (Fig. 2). Frequently, however, typical cankers do not form; instead the advancing margin of the canker is distinguished by its lighter yellowish-brown color. Water sprouts develop on infected branches below the lower margins of the canker (Fig. 2). The older portion of the cankers contains large numbers of pycnidia (Fig. 3) and during damp, rainy weather sticky spore masses exude from them. Since this type of spore is adapted for dissemination by the splashing of rain water, this may in part explain the infection and subsequent death of branches successively lower in the crown.

Diameter growth of diseased trees

Increment borings were made in a number of ash trees in various stages of decline during the summer of 1956 to determine the rate of diameter growth of affected trees. Those with the earliest evidences of dieback in 1956, as manifested by the presence of a few scattered dead branches in the crown, showed normal diameter growth through 1954 and only a slight reduction in 1955. Trees in more advanced stages of decline, as indicated by the greater number of dead branches in the crown, showed a reduction in diameter growth for a correspondingly longer period of time. Trees with no visible evidences of decline had uniform diameter growth. Active cankers may be present on many of the young branches in the upper crown before the appearance of visible dieback symptoms. Therefore, it appears that reduction in diameter growth is associated with the presence of the fungus, but not necessarily caused by the pathogen, and decreased diameter growth may precede symptoms such as dead branches by only one year.

Inoculation studies

Sixty inoculations were made on stems 1 to 3 inches d.b.h. The first 36 were made during the first week of August, and the remaining 24 during the third week of August, 1955. In addition, 6 stems from 4 to 6 inches d.b.h. and 18 branches ¾ inch or less in diameter were inoculated. Standard bark inoculation procedures were followed. The surface of the bark was first sterilized with 70 percent ethyl alcohol, and then an inverted V-shaped wedge or flap was cut through the bark with a sterile scalpel, and approximately 1 square

FIGURE 2. *Young white ash with the main stem girdled by* Cytophoma pruinosa. *The irregular margins of the canker are slightly raised and water sprouts develop near the lower limits of the canker.*

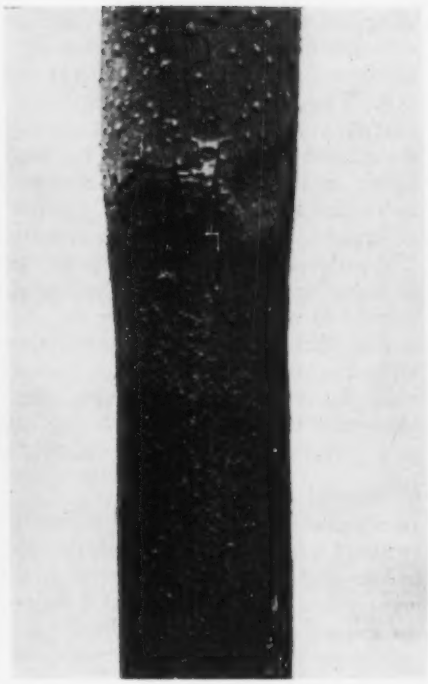

FIGURE 3. *An enlargement of a portion of Fig. 2 showing pycnidia of* Cytophoma pruinosa *developing on the older portion of the canker. Cracking of the bark is a characteristic symptom of older cankers. Pycnidia of the pathogen develop in the bark and appear as pustules on dead areas.*

centimeter of inoculum (mycelium plus malt agar) was aseptically inserted into the wound. The wedge of bark was then pressed lightly into its original position. A 3-inch square of moist absorbent cotton with a 1-inch diameter disk cut from the center was affixed so that the hole in the cotton fell directly over the inoculated wound. Controls were made in a similar fashion, but with the use of sterile agar only. Each inoculation was then covered with aluminum foil and tied with strong cord lashings.

In 9 branches up to ¾ inch in diameter the inoculum was placed directly on unwounded bark to determine whether wounds are essential for the establishment of the pathogen. Numerous stem and branch inoculations were made on sugar maple (*Acer saccharum* Marsh.), quaking aspen (*Populus tremuloides* Michx.) and black willow (*Salix nigra* Marsh.) to determine their susceptibility to the fungus.

Results of inoculation studies

Upon ash inoculated for one month, cankers up to 6 inches long and 3¼ inches wide developed on stems 1 to 3 inches in diameter. Branches up to ¾ inch in diameter were nearly girdled. This near-gir-

dling had caused disturbances in the vascular system as disclosed by the pronounced discoloration of the leaves above the cankers. The remaining leaves and branches continued normal development through the autumn weeks. *C. pruinosa* was pathogenic on 50 percent of the main stems 1 to 3 inches in diameter, and on 50 percent of branches ¾ inch or less in diameter. The pathogen was reisolated from the cankers resulting from artificial inoculations. Stems 4 to 6 inches in diameter remained free of disease. None of the controls developed cankers.

Maple, aspen and willow proved nonsusceptible when inoculated during the same period with the same fungal isolate.

Discussion

In evaluating the data gathered during the course of this investigation, two major possibilities exist. Either the fungus is the primary cause of ash dieback or it follows the dieback and may be considered a secondary pathogen. The first assumption, that of a direct or contributing agent of disease, is supported strongly by: (1) the consistent isolation of *C. pruinosa* from a large number of white ash trees; (2) the pathogenicity of the fungus as established through wounding and artificial inoculation; (3) the development of cankers with subsequent maturation of pycnidia and the production of typical dieback symptoms following artificial inoculation; and (4) the consistent reisolation of *C. pruinosa* from the cankers.

The second assumption, namely, that the fungus is a secondary agent is supported by: (1) larger stems, 4 to 6 inches d.b.h., did not develop cankers following artificial inoculation with the fungus; and (2) there may be a decrease in diameter growth before the appearance of the fungus or the first dieback symptoms. This decrease in annual increment might be an indication of widespread unfavorable environmental changes which can lower the resistance of white ash to such an extent that secondary organisms may become pathogenic.

In summarization of our present knowledge of the ash dieback disease, it can be stated that the fungus *C. pruinosa* is commonly associated with trees exhibiting dieback symptoms and appears to be an integral part of a disease complex affecting white ash.

Studies are being continued with emphasis on the spread of the disease, age of stems and branches in relation to pathogenicity of the fungus, and the use of soil fertilizers as a possible control measure.

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Ecotypic Response to Temperature and Photoperiod in Douglas-fir

BY
HELGE IRGENS-MOLLER

THE EFFECT OF changes in photoperiod upon the length of active growth period has been recognized for several years in a number of forest tree species (Moshkov, 1935; Murneek, 1948). The existence of ecotypic variations of the response to such changes has been most clearly shown by Pauley and Perry (1954).

The active height growth period is for convenience usually considered to extend from bud bursting to the formation of a dormant, terminal bud; realizing, of course, that growth in the form of cell division and cell elongation by no means is confined to this period. The photoperiodic influence upon the length of the active growth period is perhaps most pronounced in its effect on the time of height growth cessation and bud setting. This effect appears to be relatively independent of temperature conditions. Pauley and Perry (1954) have shown that *Populus* from Alaska, when grown under the shorter days of Boston, Mass., stops height growth in June in spite of otherwise optimum growing conditions. Only under artificially prolonged days is cessation of height growth prevented.

The effect of photoperiod upon time of bud bursting varies considerably with the species. Klebs (1914) showed that European beech, *Fagus sylvatica,* can be induced to break dormancy at any time by continuous illumination even without prechilling of the plants whereas it fails to break dormancy in complete darkness. Pauley (1954a) found that other members of the *Fagaceae* also fail to break dormancy in complete darkness regardless of temperature conditions. In *Populus*, on the other hand, the findings of Pauley and Perry (1954) indicate that light or its periodicity have little, if any, influence on break of dormancy. Ramets of clones grown at 70° F. and subjected, respectively, to continuous light, normal day length, and complete darkness showed no significant differences in time of bud bursting.

Bud bursting in Douglas-fir, *Pseudotsuga menziesii* (Mirb.) Franco, occurs in nature over a very wide period of time. In 1955 bud bursting at the coast of Oregon, near Newport, occurred in late April,

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The author is Graduate Research Assistant, Forest Experiment Station, Oregon State College. This paper is a progress report covering part of the first year of work of the writer's graduate thesis project while graduate assistant in the Department of Botany and Plant Pathology, Oregon State College. Continuation and extension of the project has been assured by a grant from the Forest Genetics Research Foundation to the Oregon State College Forest Experiment Station. The writer wishes to express his thanks to the Foundation for this support. Grateful acknowledgment is made to the Botany Department, Oregon State College, for use of facilities and equipment and to Dr. W. W. Chilcote and Dr. F. H. Smith for a critical review of the manuscript.

whereas in the Cascade range, at 4000 ft. above sea level, it did not occur until the middle of June. These observations refer in both cases to younger plants in which bud bursting occurs up to three weeks earlier than in older plants.

These differences would appear to be an effect of the difference in length of the growing season at the two localities. However, there is also the possibility that such differences are, in part, genetically controlled as demonstrated by Pauley (1954b) with altitudinal ecotypes of *Populus trichocarpa*. The present paper represents an effort to determine to what degree genetic factors control the time of bud bursting in Douglas-fir.

Methods and Results

Plants were collected during December, 1954 from seven localities in Oregon along an east-west transect from the Santiam Pass in the Cascades to Waldport at the coast. About 100 plants, two to six years old, were collected from each of the following locations: Snow Creek, 4000 ft.; Sheep Creek, 2000 ft.; Foster, 600 ft.; Corvallis, 300 ft.; Blodgett, 750 ft.; Summit, 800 ft.; and Tidewater, 60 ft. All plants were brought to Corvallis, potted and kept in a cold frame. Thus all plants were exposed to the same winter conditions.

During the following spring the date of bud bursting for each plant was noted. Date of bud bursting is defined as the day in which the needles of any bud, regardless of the position on the plant, first emerge from between the bud scales. In most plants the terminal bud on the leader was the first to burst, but in a few plants buds on lateral branches were earlier than the terminal. Plants with a damaged terminal bud or leader were discarded since damage to, or removal of the leader, may induce early bud bursting (Bünning, 1948). Observations were made each day during the bud bursting period (Fig. 1).

The high altitude plants were the latest in bud bursting and the plants from Cor-

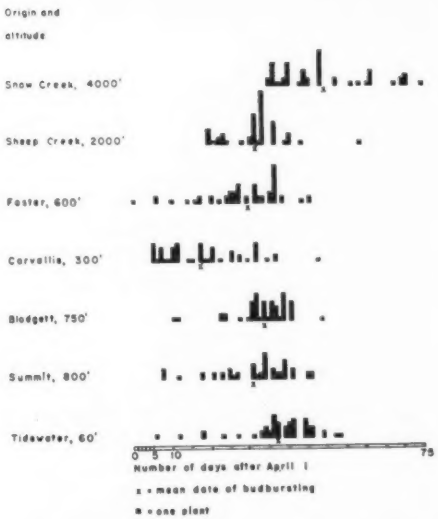

FIGURE 1: *Dates of bud bursting of Douglas-fir seedlings from seven different localities in Oregon when grown at Corvallis, Oregon, spring 1955.*

vallis the earliest. According to these data, there appears to be some correlation between date of bud bursting and altitude (or length of growing season) of origin. A multiple range F-test as devised by Duncan (1955) shows that the mean date of bud bursting for the plants from Corvallis (300 ft., 20 days after April 1) is significantly different from any of the other means. The same is the case for the plants from Snow Creek (4,000 ft., 51 days after April 1). The plants from Tidewater (60 ft., 38 days) differ significantly from those of all other localities with exception of those from Blodgett (750 ft., 35 days). No significant difference exists among the plants from Foster (600 ft., 31 days), Summit (800 ft., 32 days), Sheep Creek (2,000 ft., 33 days) and Blodgett.

The uniform treatment given all plants during the preceding winter may not have been of sufficient duration to remove any preconditioning effect developed prior to their collection. All plants were therefore left in the coldframe for another year.

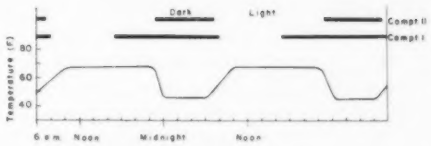

FIGURE 2: *Temperatures and day lengths employed in experiment in temperature controlled compartments. The day length in compartment II increased gradually from 15 hours 15 minutes to 17 hours 45 minutes during the experiment.*

On February 1st, 1956 half of the plants from each locality were removed to temperature controlled compartments. In compartment I, the plants were exposed to normal daylight from 8 a.m. to 5 p.m. and covered with light-proof black cloth from 5 p.m. to 8 a.m. In compartment II, the plants were exposed to normal daylight from 8 a.m. to 5 p.m. and to artificial light from a 200 Watt bulb from 5 p.m. to 11 p.m. The temperature in both compartments was kept at 45° F. during nights and at 65° to 70° F. during days. The treatments are graphically illustrated in Fig. 2.

Date of bud bursting was noted for each plant (Fig. 3). For the low altitude plants (Corvallis and Tidewater) no significant differences exist between the two treatments. The high altitude plants, on the other hand, show significant differences between the treatments. Although a longer photoperiod did not significantly change the mean date of bud bursting of the low altitude plants, long days did hasten bud bursting strikingly in the high altitude plants. This effect of longer days upon the bud bursting of high altitude plants could conceivably account for the lateness in bud bursting of high altitude plants observed the previous spring (Fig. 1).

The remaining plants from each locality were left in the coldframe. Half of them were exposed to normal day, and the other half received additional light from 5 p.m. to 11 p.m. The temperatures to which these plants were exposed were recorded by thermograph and are shown in Fig. 4. The differences in mean dates of bud bursting between the two treatments in this experiment are much smaller (Fig. 5) than in the previous one. None of them are statistically significant. But it will be seen that where there are differences it is consistently the long day treated plants which have the earliest means. The smaller differences in this experiment may be due to the fact that the difference in day length between the two treatments was less than in the previous experiment (cf. Fig. 2 and Fig. 4). Another reason may be the different temperature regimes under which the two experiments were conducted. The plants in the temperature controlled compartments were consistently exposed to 45° F. for six hours each night and to day

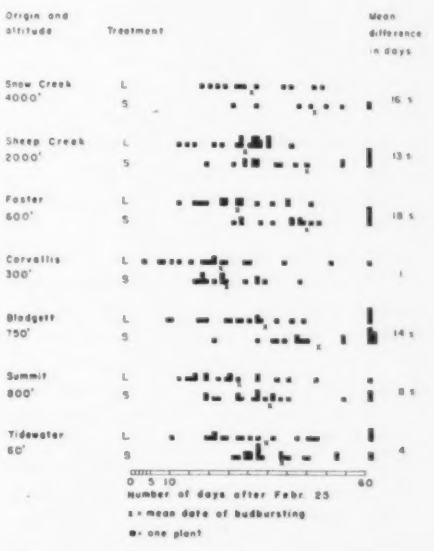

FIGURE 3: *Dates of bud bursting of Douglas-fir seedlings from seven different localities in Oregon when treated with the temperatures and day lengths shown in Fig. 2. L = long days, S = short days, s = mean difference is significant at the 5 percent level of significance (t-test). Spring 1956.*

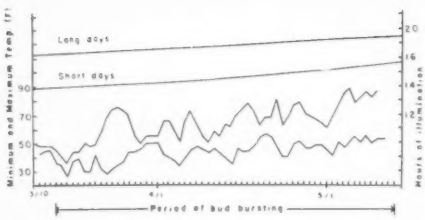

FIGURE 4. *Temperatures and day lengths to which Douglas-fir seedlings in coldframes were exposed (see text).*

temperatures between 65° and 75° F. The plants in the coldframe, on the other hand, were during the first month of the experiment seldom exposed to temperatures above 45° F. while in the latter half of the experiment the day temperature often went considerably above 70° F. and the night temperature only occasionally went down to 45° F. and then only for brief periods (Fig. 4). These high temperatures may act as a compensating factor for the long-day requirement thus reducing the difference in time of bud bursting between the plants exposed to long and short days, respectively. It is well known from agricultural crops (Murneek, 1948) that photoperiodic sensitivity may be lost at high temperatures.

No experiments with high temperatures day and night, utilizing plants from the same sources as in the previous experiments, were possible due to the limited number of plants available. However, plants from high elevation (4,200 ft.) and low elevation (1,500 ft.) from the vicinity of Roseburg, Oregon, about 100 miles south of Corvallis, were used in an experiment in which half of the plants from each source were exposed to nine hours of normal daylight and the other halves to an artificially prolonged day (18 hours of illumination). Both treatments were conducted in a greenhouse at a temperature of approximately 70° F. day and night during the months of March and April, 1956. No significant differences in dates of bud bursting were found between the two treatments for either the low altitude or the high altitude plants. Although this experiment, due to the different source of plants, does not furnish conclusive evidence for the compensating effect of high temperatures it appears reasonable to accept it as a working hypothesis to be verified by further experiments.

Discussion

What are the ecological implications of these results and how are they related to movements of planting stock to altitudes different from that of their place of origin?

High altitude plants of Douglas-fir appear to have a definite photoperiodic response with regard to date of bud bursting. The magnitude of this response appears to be increased if the plants are exposed to low night temperatures and may disappear if exposed to high day and night temperatures.

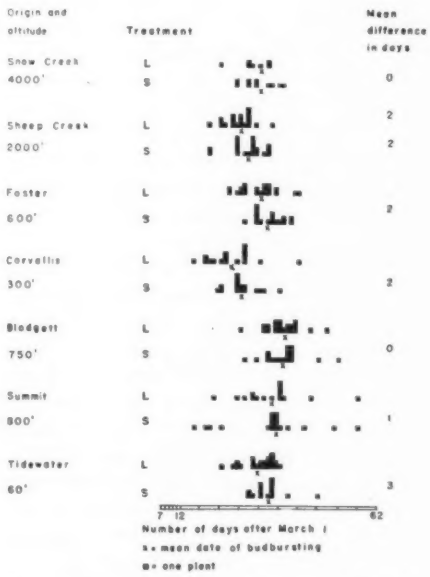

FIGURE 5: *Dates of bud bursting of Douglas-fir seedlings from seven different localities when grown under long (L) and short (S) days without temperature control. Spring 1956.*

These experimental results have led to the following tentative hypothesis, which will require verification by more extensive experiments. Compared with that of the lowlands, the climate in high altitudes is characterized by widely fluctuating day and night temperatures. This was shown by thermographs placed at five of the localities during the spring of 1955. During early spring there may often be several warm days in succession at a time when the night temperature goes below freezing. These high day temperatures could conceivably induce bud bursting activity leading to frost damage during nights. However, the cold nights in high altitudes may result, as shown by the experiments, in photoperiodic sensitivity of plants native to high altitudes in the sense that a longer day is required for bud bursting. When the required longer days arrive later in spring bud bursting will occur rapidly. The natural selection to which Douglas-fir in high altitudes have been exposed may have resulted in plants for which the optimum length of day for bud bursting occurs at a time when the danger of night frost usually is low.

The plants in the lowlands, where the daily temperature fluctuations are considerably smaller, have not been exposed to a similar selection. This might explain the lack of influence of a long photoperiod upon the date of bud bursting found in the present experiments for the plants from low altitudes.

Since these experiments employed seedlings the results become somewhat obscured by the genetic heterogeneity found inside each group of plants. In order to demonstrate more clearly the influence of temperature upon the photoperiodic response it would be necessary to work with genetically uniform material. Such an attempt is presently being made by the establishment of clones.

If the above hypothesis is substantiated by further experiments it may have an important bearing upon the interpretation of results obtained when low altitude plants are moved to high altitudes and vice versa.

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Observations on Yellow-poplar Dieback

BY
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M. H. GOFORTH
R. W. POWELL, JR.
N. D. HAAR

DIEBACK and associated stem canker of yellow-poplar saplings (*Liriodendron tulipfera* L.) was first described by Toole and Huckenpahler,[1] who reported that " . . . considerable mortality was found associated with the disease . . . " in some stands. They isolated a nonsporulating fungus from the trunk and branch cankers, and found that a *Myxosporium* was associated with dead bark of infected trees. Seventy-five percent of their experimental inoculations with this *Myxosporium* resulted in canker formation.

Yellow-poplar dieback, first observed in Mississippi, has since been found by the senior author in scattered localities in Louisiana, southwestern Tennessee, north-central Alabama, and in the North Carolina Piedmont. Several yellow-poplar stands in the Duke Forest showed a high percentage of infected trees. Hence, in September, 1954, a study was initiated to determine (1) if the disease was the same as that described by Toole and Huckenpahler; (2) if a causal organism could be isolated, and (3) if the organism isolated by Toole and Huckenpahler did induce symptoms of the disease similar to those on naturally infected trees. The principal concern in this study was with intensity and damage in natural and planted stands in the Durham Division of the Duke Forest, Durham and Orange Counties, North Carolina.

Symptomatology and Etiology

The symptoms of yellow-poplar dieback in the Duke Forest are identical with those described by Toole and Huckenpahler: chlorotic atrophism of leaves, sparse crown, dieback, trunk and branch cankers, and epicormic sprouting. Periodic observations on the development of the disease in the Duke Forest show a rather characteristic and consistent progression of symptoms. Dieback begins either in the lowermost or uppermost crown branches, and in naturally infected saplings always progresses inward and downward toward the trunk. Epicormic sprouts occur on approximately 60 percent of the infected trees. Such sprouts on saplings are successively killed, and the bark may then exhibit symptoms suggestive of frost shake.

As the stem cankers enlarge, lateral bark cracks occur which are similar in appearance to frost cracks. In small crown branches the cankers enlarge rapidly and girdle the branches. Bole cankers, in the early stages, are similar to those on the

[1]Toole, E. R., and B. J. Huckenpahler. 1954. Yellow-poplar dieback. Plant Dis. Reptr. 38(11): 786-788.

Contribution from the Department of Botany and School of Forestry, Duke University, Durham, North Carolina. We are grateful to Drs. F. A. Wolf, H. J. Oosting, J. S. Boyce, Jr., A. W. Poitras, and J. A. Schmitt, Jr., for their critical review of the manuscript.

crown branches. As the cankers enlarge, they become ellipsoid-elongate, and generally increase more rapidly along the length of the bole than around it. The secondary phloem is killed and the underlying sapwood is discolored. Cankers which have not completely girdled the tree are sharply defined. Cankers appear progressively from the crown branches downward to the root collar. Occasionally a trunk may have only a single canker near the root collar; more commonly, several cankers are in evidence. In the latter instances, the lowermost canker marks the limit between the living and dead portion of the trunk.

As infection progresses, the sapwood becomes light brown, changing to a "dirty-gray" as the wood dries. The juncture between infected and noninfected wood is clearly defined. Definite cankers commonly do not develop on epicormic branches, but these are killed rapidly as the infection grows up and down the stem.

Three sporulating and several nonsporulating fungi have been isolated repeatedly from cankers. *Pestalotia sp.* produces acervuli on the bark covering young cankers, and occasionally that of older, ruptured cankers. This fungus can usually be isolated from the dry, discolored sapwood. Two fungi, tentatively identified as members of the genus *Myxosporium*, were also isolated from the juncture between discolored and "normal" sapwood. They have not sporulated in culture, but the inference from the presence of *Myxosporium* fructifications on dead and living bark around the cankers suggests that the mycelial isolates are possibly members of this genus. Two isolates of *Myxosporium* from small cankers have sporulated sparingly on Nutramigen agar. The third sporulating fungus, isolated only from very young cankers, either in the inner bark or the outer sapwood growth ring, is *Cladosporium cladosporioides*.[2]

[2]DeVries, G. A. 1952. Contribution to the knowledge of the genus *Cladosporium* Link ex Fr. 121 pp. Centraalbureau voor Schimmelcultures, Baarn.

All nonsporulating isolates were propagated on Sabouraud-dextrose, 2 percent cornmeal, PDA, 2 percent V-8 juice, 1 percent starch, yellow-poplar sawdust extract, 2 percent Czapek-Dox, and Blakeslee's agars. Sporulation was not induced in colonies on any of these media.

Associated with the sapwood immediately below the trunk cankers are black, soft, irregular areas which always harbor yellow chromogenic bacteria. Furthermore, in all isolations from the juncture between discolored sapwood and "normal" sapwood, yellow bacterial colonies appear with those of fungus mycelium. Three unidentified species of bacteria associated with cankers and the subtending blackened areas have been isolated. One of these is a species of *Xanthomonas*. The remaining two bacterial isolates have not been identified; they are similar to one another in physiological reactions, both are pale yellow chromogens, but are different in morphology. Since the *Xanthomonas* is the most likely pathogen of the three, a brief description is given:

Gram negative motile rods, 1.2-2 μ long X 0.4-0.6 μ in diameter; colonies smooth, shiny, entire, raised, lemon-yellow; gelatin liquified, starch hydrolysed, milk peptonized. hydrogen sulfide produced; indole not produced, nitrate not reduced; acid but no gas from glucose, sucrose, mannitol, and glycerol.[3]

Epidemiology

Yellow-poplar dieback is prevalent throughout the Duke Forest except in stands with trees over 12-14 in. d.b.h. Saplings under 6 in. d.b.h., and in a few instances 1-1 seedlings, are most severely damaged. A survey of the Durham Division was made to ascertain extent and severity of infection.

The data in Table 1 are from 10 of 18 observation plots where a detailed analysis of the stand was made. In addition, 25 other stands of yellow-poplar were examined and the prevalence of dieback esti-

[3]At 24 and 48-hour incubation, 37° C.

TABLE 1. Prevalence of yellow-poplar dieback in the Durham Division.

Site	Number of trees	Percent infected	Average d.b.h. (inches) of infected trees	Average d.b.h. (inches) of noninfected trees
2	18	50	2.6	2.7
9	13	54	3.7	8.5
10	26	60	2.8	6.1
17	24	53	2.7	5.8
20	33	36	2.0	1.8
23	20	45	3.1	4.9
24	8	75	3.9	3.4
27	29	55	3.7	4.0
31	29	17	1.6	6.8
33	21	14	1.9	5.9

mated. In two planted stands no dieback was observed on trees over 8 in. d.b.h., but many smaller saplings (under 3 in. d.b.h.) were dead. Three young stands were free of the disease. On all other sites, consisting of uneven-aged yellow-poplar in mixed stands, canker and dieback was observed. Mortality from the disease ranged from 2 dead trees in a stand of 26 trees to 21 dead trees in a stand of 23.

Observations indicate that trees larger than 6 in. d.b.h. are not as susceptible to dieback as are smaller ones. This conclusion must be conditioned by the possibility that larger trees had previously been infected and had recovered, or that cankers were present in the crown but were not visible by ground observation. In mild attacks, small, localized cankers may be present in the crown branches but the dieback symptom is not immediately apparent.

In certain yellow-poplar stands the incidence of dieback was found to have increased in two years; conversely, in others, there was no increase, or, in some instances, apparent partial recovery (Table 2).

Both upland and bottomland sites are represented in the five plots shown in Table 2; none of the plots were in pure stands. Plot 4, for example, consisted of yellow-poplar, sweetgum, and uneven-aged loblolly pine, in upland, well-drained soil. Plot 2 on the other hand, consisting principally of the same tree species, was in poorly drained bottomland, with a dense ground cover of *Smilax* and *Lonicera*. Except in plots 5 and 6, the disease increased considerably over a 2-year period. In plot 6, having trees averaging 5.1 in. d.b.h., there was no increase, and at least one of the infected trees showed definite evidence of canker healing and recovery.

The rapidity of dieback development in individual trees varied considerably (Table 3). In certain trees the rate of spread, concomitant with the formation of new cankers, is rapid, particularly in those with a small diameter (Table 3, last entry). Spread of infection in larger trees is generally slow, but exceptions do occur (Table 3). The data give no indication of the time lapse between inoculation and death, although some trees with slight initial infection may be killed in two years.

Inoculations

A limited number of field inoculations were made using the Mississippi isolate obtained by Toole and Huckenpahler, and the three fungal isolates from cankered trees in the Duke Forest, YPD 1, 2, and 19. Two of the latter three were nonsporulating but were identical in culture with the original Mississippi isolate. All trees were inoculated at breast height with mycelium from 8-day-old Nutraamigen agar cultures. Inoculum was placed in the center of an X-shaped

TABLE 2. Increase of yellow-poplar dieback, 1954-1956, on 5 observation plots.

Plot	Number of trees	Number infected 10/8/54	Number infected 6/10/56	Number dead 10/8/54	Number dead 6/10/56
1	22	6	12	0	3
2	16	3	14	1	4
4	36	4	27	3	11
5	19	2	5	0	0
6	13	2	2	1	1

TABLE 3. Spread of infection in individual trees, evidenced by increase in number of cankers.

Tree diameter, breast height (inches)	Date of initial observation	Initial number of cankers	Number of cankers in 6 months	Number of cankers in 12 months	Date tree dead
6.3	6/6/55	3	8	12	.....
2.8	6/6/55	0	3	4	.....
3.3	1/16/56	2	8	...	.....
3.6	10/10/54	3	10	14	6/10/56
3.3	1/12/55	1	16	18	6/10/56
1.9	3/15/55	4	6	29	3/15/56
1.1	3/15/55	1	11	31+	3/15/56
5.1	9/23/54	18	18	21	.....
1.8	6/19/55	0	21	28+	7/10/56
3.1	6/20/55	1	9	9	.....
6.1	10/10/54	7	9	23+	5/18/55
1.0	10/10/54	3	27	38+	.....

wound, directly on the current year's sapwood. The inoculation site was covered with a plastic sheet. Trees selected for inoculation were in stands where neither the selected trees nor immediately adjacent ones showed dieback or canker symptoms. Only three inoculations failed. Seven inoculated trees were subsequently eliminated from consideration because adjacent trees became naturally infected. The results of the artificial inoculations are given in Table 4.

All of the isolates induced canker formation at the original site of inoculation, and generally other cankers subsequently developed. Three trees greater than 5 in. d.b.h. were successfully inoculated, but no new cankers developed. Two saplings were very severely infected by the inoculation (9 and 28, Table 4). The possibility exists (in the case of tree 9, for instance) that cankers developing other than at the site of inoculation could have been induced by naturally occurring inoculum. The probability of natural infection, however, is less certain since adjacent trees did not exhibit symptoms, at least during the time from inoculation of the test tree to the terminal observation. This evidence does not, of course, preclude the possibility of root infection. In none of the cankers induced at the original site of inoculation were the black, soft areas developed in the sapwood, and no yellow chromogens could be isolated from these cankers. Similarly, no bacterial damage could be detected in cankers developing after the artificially-induced canker appeared. Only a very few secondary cankers were checked for bacteria, however. The fungi used as inoculum (insofar as an examination of cultural and vegetative characteristics revealed) were reisolated from 15 of the test trees. Of the inoculated trees, only tree 9 (Table 4) showed dieback symptoms.

Site and Stand Factors

Most of the yellow-poplar stands examined were along creeks and intermittent streams. Although the suscept is not confined to bottomland, its best development is there. Dieback is occasionally severe on trees on ridge or slope sites. Generally, the severity and extent of infection is greater in upland sites than in bottomland sites. This observation is conditioned by the fact that the trees in upland stands are scattered and less vigorous than those of the lowland stands.

Soil factors are known to be the limiting ones in site quality differences for many tree species. In some diseases (little-leaf and loblolly spot die-out, for instance) severity is correlated in part with soil factors. The Durham Division has been

TABLE 4. Artificial inoculation of yellow-poplar with four isolates from infected trees.

Tree	Isolate	Date of inoculation	D.b.h. (inches) of inoculated tree	Number of days before infection noted	Number of new cankers June 1956
1	Miss 1	9/19/54	3.0	212	3
2	Miss 1	9/19/54	1.1	212	6
3	Miss 1	9/19/54	2.6	109	1
4	Miss 1	10/31/54	5.1	212	0
7	Miss 1	1/12/55	6.7	219	1
9	YPD-1	1/12/55	1.4	189	21
10	YPD-1	1/12/55	0.6	189	0
11	YPD-1	4/18/55	0.5	89	4
16	YPD-1	4/18/55	2.3	154	3
20	YPD-1	4/18/55	2.6	154	5
21	YPD-1	5/3/55	4.1	92	9
22	YPD-2	5/3/55	3.2	148	1
23	YPD-2	5/3/55	3.2	238	3
24	YPD-2	1/21/56	5.9	141	0
26	YPD-19	9/10/55	1.7	175	2
27	YPD-19	11/19/56	2.8	105	3
28	YPD-19	1/21/56	0.5	141	Dead

completely typed as to soil, and in the majority of yellow-poplar stands there was little difference in site factors other than soil type. Although dieback is more prevalent on trees in Worsham and Triassic soils than on the more common Congaree type, there is at present no suitable explanation for this occurrence.

In this area yellow-poplar is not commonly found in pure stands except in managed plantations. It is usually mixed with sweet-gum, and in some stands with sycamore, red maple, dogwood, and pine. From recorded data and from unrecorded observations, it is apparent that dieback is more prevalent in mixed stands of pine and yellow-poplar than in mixed stands of sweet-gum and yellow-poplar. In the former, which usually occur on slopes or ridges, the pines overtop the poplar. Plantations generally exhibit less severe infection than do stands of natural regeneration. This may be causally related to the fact that planted stands are usually managed to reduce competition from both vines and other tree species.

Discussion

Yellow-poplar dieback and canker disease is common in the Duke Forest, where it occurs to some extent in almost all stands of the suscept. Whether or not the canker and dieback symptoms are actually the expression of a single disease is not known for certain. It is conceivable that the two symptoms are the expression of infection by two different causal organisms or agents. Similarly, nothing is known about factors involved in the onset of the disease. The aspect of some infected trees suggests that the disease symptoms are reactions to secondary invaders; conversely, there is no doubt that at least one organism induces symptoms, in vigorous trees, which are precisely the same as those expressed by naturally infected trees. Regarding mode of entrance and the source of inoculum, nothing has been established. It is clear, however, that some trees become infected through the crown, suggesting that the inoculum is air-borne. The possibility of root infection is not excluded.

Numerous factors, both environmental and internal in the suscept, must be studied thoroughly. Small, thrifty trees (1-3 in. d.b.h.) seem less susceptible than small (1-4 in. d.b.h.) less vigorous ones. The frequent occurrence of severe infection in vigorous saplings in well-managed yellow-poplar sites, however, prevents the conclusion that dieback is always associated with low suscept vigor. A detailed soil study is needed to determine the influence of soil factors on disease intensity. Mode of spread, factors influencing or inducing sporulation of the organisms involved, and the influence of host age, are other factors which must be investigated.

Toole and Huckenpahler implied in their original publication on yellow-poplar dieback that a species of *Myxosporium* was the probable causal organism. This supposition is stated in somewhat more definite terms in the 1955 Annual Report of the Southern Forest Experiment Station (p. 48). Conclusive evidence is lacking that the fungus consistently isolated from cankers (on trees in the Duke Forest) is a single species or that it is even a *Myxosporium*, since only two of the isolates sporulated in culture. The evidence that the causal organism is a *Myxosporium* seems principally circumstantial at the present time. Inferring from the presence of fungus mycelium and bacteria in isolation cultures from cankers, it is entirely reasonable to suspect that the cankers, if not the dieback, develop as the result of the activity of a fungus and a bacterium. Inoculation of suscepts with two-membered cultures should give data to support or refute this supposition. Certainly the results of experimental inoculations do not presently support this hypothesis. Under laboratory conditions it has been possible to induce discoloration and degradation of freshly-cut yellow-poplar sapwood by inoculation with the *Xanthomonas* sp.

In view of the severity of yellow-poplar dieback in the Duke Forest, the presence of the disease in four southern states, and the economic importance of the suscept, it is believed that the disease is worthy of an intensive and detailed investigation. Until such time as it has definitely been established that the disease is one of mere enphytotic proportions, it seems advisable to regard it as a potential epiphytotic, and investigate it accordingly.

Summary

Results of a two-year study of yellow-poplar dieback in the Duke Forest are reported. Three sporulating fungi, several nonsporulating ones, and an undetermined species of *Xanthomonas* were consistently isolated from cankered trees. The disease affects trees in somewhat isolated groups. Severity ranges from single, isolated cankers on less vigorous understory saplings to a high percentage of mortality in stands of vigorous trees up to 6 in. d.b.h. The disease is relatively more severe in upland sites (particularly in mixed stands of pine and yellow-poplar) than in bottomland stands, and the intensity of infection within a stand is not in proportion to the extent of that stand. Site may be a determining factor in severity, particularly if coupled with a high degree of competition.

Studies of Attack by Ambrosia Beetles in Softwood Logs on Vancouver Island, British Columbia

BY
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THE AMBROSIA BEETLES, comprising some members of the family Scolytidae and all members of the family Platypodidae, are woodboring insects whose young develop in galleries constructed by the parents. The walls of the small circular galleries are lined with fungous growth (ambrosia) upon which the insects feed. The wood surrounding the galleries becomes heavily stained as a result of the fungous growth. Ambrosia beetles are widely distributed and commonly attack dying and dead trees, logs, stumps, and logging slash. Less commonly they attack sawn lumber. A review of the world literature on the biology, habits, and control of these insects has recently been published by Fisher, Thompson, and Webb (1953, 1954).

The galleries made by ambrosia beetles constitute a serious defect in the manufacture and sale of products from infested logs, which accordingly have a reduced value on the log market. Under scaling practice in British Columbia, the mill scaler is authorized to deduct one or two inches from the diameter of infested logs to compensate for the injury. Since he is not required to record such deductions there is no official estimate of the loss to the log producer resulting from ambrosia beetle attack. The effects of attack on the manufacturing of infested logs, on the grade and value of lumber produced, and its saleability in the export market, have been described by Graham and Boyes (1950) and McBride (1950). In the milling of infested peeler logs, veneer from the outer portion is reduced from high value face stock to low value core stock for plywood manufacture.

In British Columbia, ambrosia beetles attack "green" wood, after death or injury to the tree, or after felling and bucking into logs. Characteristically they attack through the bark, but they may enter wood exposed by breakage of the bark or by saw cuts. Occasionally they attack freshly sawn lumber in mill yards, and the exposed surface of logs floating in water. In the coastal area of the Province, fresh attacks by the various species occur from early April until November, in logs cut from a few days to two years, or longer, before the time of attack. The gallery pattern, and the rate and ultimate depth of penetration into the wood, vary in the different species of ambrosia beetles, and are in some

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cases influenced by the sapwood thickness of the host log.

The investigations described here were undertaken to derive quantitative estimates of the intensity of attack by the different ambrosia beetles in relation to time of felling and period of exposure, and to provide a measure of the resultant damage in the logs. Periodic examinations of infested logs were carried out on Vancouver Island from 1942 to 1945. Special thanks are due J. W. Challenger, of MacMillan and Bloedel Limited, and T. M. Fraser, of British Columbia Forest Products Limited, for their interest in the investigations, accommodation at logging camps, and permission to cut log sections in various logging operations conducted by their employers at that time, namely, Bloedel, Stewart and Welch Limited, and Industrial Timber Mills Limited, respectively. The assistance of R. L. Fiddick, of the Forest Biology Laboratory, Victoria, in field studies in 1945 is gratefully acknowledged. We are indebted to S. L. Wood and O. Peck, of the Systematic Unit of the Entomology Division, Department of Agriculture, Ottawa, for information on the taxonomy of the genus *Trypodendron*, and for assistance leading to the identification of the parasite *Eurytoma polygraphi*, respectively.

Life History and Habits of the Beetles

At least five species of ambrosia beetles were encountered in softwood logs on Vancover Island. Although many observations have been made on these insects, and a few detailed studies have been carried out, many features of their biology are still obscure. The following general accounts of their life histories are based in part on observations during the course of the studies reported here, and on earlier unpublished studies by Graham in 1934 and Mathers in 1935.[1]

Platypus wilsoni Swaine

This species is the only member of the family Platypodidae known to occur in Canada. The beetle is about 5.5 mm. long by 1.3 to 1.5 mm. wide; the head is visible from above, and in the male the wing covers project in spine-like tips behind. It is dark mahogany-brown in color. Recorded hosts in British Columbia include Douglas fir [*Pseudotsuga menziesii* (Mirb.) Franco], western hemlock [*Tsuga heterophylla* (Raf.) Sarg.], grand fir [*Abies grandis* (Dougl.) Lindl.], and amabilis fir [*Abies amabilis* (Dougl.) Forb.]. In the southern coastal area of the Province, attacks are started from about the third week of July until mid-September. The beetles enter logs within three weeks of the date of felling to as late as 31 months after felling. They rarely attack logs smaller than 11 inches in diameter. Stumps appear to be relatively free of attack.

The male beetle commences the gallery and may bore to a depth of an inch or more before being joined by the female, which then undertakes the extension of the gallery. The initial rate of boring may reach 3 inches per week. The gallery is at first simple, and winds through the sapwood into the heartwood to a depth of 8 inches or more. New tunnels are added to the gallery system in the 18-month period following initial attack, and a completed gallery system may contain as many as nine tunnels, all lying in one plane at right angles to the long axis of the log. The galleries are distinguishable from those of the other ambrosia beetles by their complexity, non-conformity to the arc of the annual rings, and the square-cut gallery end (concave in the other species). Tiny splinters are included in the boring dust ejected by the excavating beetles, but when fresh excavation is not in progress the dust from the galleries is pellet-like, the splinters being absent. Growth of ambrosia fungus has been observed when the galleries are about 4 inches long. Staining of the gallery walls appears in the second season, and is less conspicuous in the heartwood than in the sapwood.

Egg laying starts during the first month of gallery formation. The eggs are white, opalescent, 0.88 mm. by 0.6 mm., and are

[1] Forest Biology Laboratory, Vernon, B.C.

laid loosely at the end of the tunnel, in groups of about 20 to 40 or more. The newly emerged larvae are white and legless, the head being wider than the body. They travel with equal facility forwards or backwards in the gallery. In later stages, they become more nearly cylindrical and less active. Larval development requires a year or more in southern British Columbia. Pupal chambers are cut in the walls of the gallery parallel to the grain. Larvae and adults overwinter in the logs.

***Trypodendron* spp.**

Trypodendron lineatum (Oliver) is the valid name for ambrosia beetles hitherto known as *T. cavifrons* (Mannh.), *T. bivittatum* (Kirby), *T. borealis* Swaine, and *T. vittiger* (Eichh.).[2] Although *T. lineatum* is the predominant species where these studies were carried out, *T. ponderosae* Swaine and *T. rufitarsis* (Kirby) also occur in the area and may have formed part of the populations whose attack and damage were investigated. The species are very similar in habits, and difficult to distinguish.

The beetles are about 3.5 mm. long by 1.5 mm. wide. The head is well rounded in the female, concave in front in the male, and concealed from above by the prothorax. The beetles are dark brown to black with lighter longitudinal bands along the elytra. Known hosts include Douglas fir, amabilis fir, grand fir, western hemlock, western red cedar (*Thuja plicata* Donn), spruce (*Picea* spp.), and pine (*Pinus* spp.).

Intensive studies of the anatomy and biology of *T. lineatum* (*Xyloterus lineatus*) were carried out in Switzerland by Hadorn (1933). Similar studies are being conducted on Vancouver Island (Kinghorn and Chapman, 1954; Chapman, 1955a, b) to provide the basis for control operations. Initial flights of the beetles occur from late March to early May, depending on the time of rapid rise in maximum daily temperature. These initial flights are the heaviest of the season and are followed by concentrated attack in susceptible logs. Lighter flights and attacks occur later, from mid-June until August. The beetles attack logs in shade, fully exposed logs in clearcut areas, and the exposed portion of floating logs. Over 250 entries per square foot have been recorded in certain Douglas fir logs. Stumps are also heavily attacked.

The galleries are begun by the female beetles, usually in bark crevices, and are completed in about three weeks. They are usually forked, with two, or less frequently three, branches. The galleries typically extend obliquely across the annual rings, but occasionally one of the branches follows an annual ring close to the outside of the log. The entire gallery system lies in one plane at right angles to the grain of the wood. The gallery walls become blackened by the ambrosia fungus within a few weeks of the initiation of attack.

Oviposition commences in the first two weeks of gallery construction. The white, translucent eggs, about 1.0 mm. by 0.72 mm., are laid individually in niches cut into the end grain of the wood at intervals along the galleries. Hatching occurs after about 10 days. As the white, legless larvae grow they enlarge the egg niches into larval cradles, within which pupation occurs about three weeks after hatching. The pupal stadium is about ten days. Young adults emerge from the log and overwinter in the duff, principally near the edge of adjacent standing timber.

The parasite *Eurytoma polygraphi* (Ashm.) has been recovered twice from Trypodendron in British Columbia. In 1932, this species parasitized about 2 per cent of the Trypodendron larval brood in hemlock logs near Mission.[3] In 1943, very light parasitism occurred in Douglas fir logs studied by the authors at Great Central Lake. These appear to be the only Canadian records of this parasite.

[2] Personal communication from S. L. Wood, Entomology Division, Department of Agriculture, Ottawa.

[3] Hopping, G. R. 1932. Unpublished report. Forest Biology Laboratory, Vernon, B.C.

Gnathotrichus sulcatus Lec.

The beetle is about 4.5 mm. long by 1.3 mm. wide, and is dark reddish-brown. The front of the head is marked by prominent, convergent aciculations. In contrast, the front of the head in the closely related *G. retusus* Lec. is punctured in the female, and smooth with feeble aciculations in the male.

Gnathotrichus sulcatus attacks Douglas fir, amabilis fir, grand fir, western hemlock, western red cedar, yellow cedar [*Chamaecyparis nootkatensis* (D. Don) Spach], and various pines and spruces. The beetles are commonly in flight about one or two weeks later in the spring than Trypodendron. The first new galleries of the season are started from early April to late May. Unlike the heavily concentrated attacks of Trypodendron, those of Gnathotrichus are at first light, gradually reach a peak, and then taper off. Later in the summer and autumn, there is a second wave of attacks which are usually made in logs not attacked in the spring flight.

Boring of the gallery is started by the male beetle, but this function is soon taken over by the female. Variable rates of penetration have been noted, from less than ½ to over 1¼ inches per week. The excavation of the gallery system may continue for a year or more as new branch galleries are added. The entire gallery system lies in one plane at right angles to the grain. Spherical, black-stalked fruiting bodies of the ambrosia fungus have been detected about a month after initiation of attack. Later, the fungus growth turns yellow, finally black, and the wood is stained black for about one-fifth inch around the gallery.

White, ellipsoidal eggs are laid in individual niches cut in the end grain of the wood along the galleries, and are packed in with fine chips. As many as 60 eggs may be found in a single gallery system. The larvae are white and legless, and enlarge the niches as they grow, and subsequently pupate therein. The parent beetles keep the entire gallery system clear by ejecting boring dust to the outside. All stages of the insect overwinter within the log. Eggs deposited in mid-summer give rise to young beetles the following spring. The young beetles feed upon the ambrosia fungus before they emerge to start new attacks.

The habits of *Gnathotrichus retusus* Lec. are similar to those of *G. sulcatus*. In the course of this study, the former species was encountered only in a few logs at Cowichan Lake and Great Central Lake in 1942.

Xyleborinus tsugae Swaine

This small beetle, about 2.4 mm. long and 0.8 mm. wide, is readily distinguished from the other ambrosia beetles by size alone. It is dark reddish-brown to almost black. It attacks Douglas fir, amabilis fir and western hemlock from the latter part of May to late August.

The gallery system is relatively simple. The entrance tunnel extends radially for a distance of less than ¼ to over 1½ inches. From the side or end there is constructed a branch tunnel which may follow an annual ring. The parent beetles occasionally enter a Gnathotrichus gallery, and construct their own gallery system as an offshoot. Eggs are deposited freely in the gallery, in groups of as many as 48, and the ensuing larvae develop togther in a communal chamber at the end of the gallery. It is not known whether the parent beetles excavate the communal chamber, which is of considerably greater diameter than the minute entrance gallery. Larvae, pupae, and young adults overwinter in the logs.

Methods

The investigations were restricted to felled-and-bucked Douglas fir, western hemlock, and amabilis fir logs in clear-cut areas, or along right-of-ways. Some of the logs had been moved aside from the right-of-ways, but all logs lay close to the ground, subject to shading only from other logs or the adjacent margin of standing timber. Log analyses were carried out at Cowichan Lake in 1942 and 1943; at Great Central Lake in 1942, 1943, and 1944; and at

Sproat Lake, and Port Alice in the Quatsino area, in 1945. Time of felling was ascertained from company records, and logs were sectioned periodically after each felling date. The 630 logs sectioned in this study comprised 96 lots representing the three timber species, different felling dates, and subsequent exposure periods.

In the preparation of logs for analysis, a 6-inch section at the end was sawn off and discarded, to avoid broken ends and the possible influence of drier wood on beetle attack or development. The adjacent 12-inch block was sawn off for analysis. Although two or more blocks were frequently taken from various logs originating from one tree, there was no deliberate attempt to confine the sampling to one portion of the bole, or to extend it proportionately to all parts of the bole. The end of the block was marked into quarters on either side of the vertical diameter line, the first quarter being in the upper half and on the most exposed side (southeast to west). The second, third, and fourth quarters followed in sequence, clockwise. The bark was then stripped off and the number of attacks by each species of ambrosia beetle was recorded separately for each quadrant.

Many galleries were studied in detail. Notes were made on the presence or absence of the parent beetles and on brood development, and measurements were taken of the depth of penetration and the lateral extent of the gallery system. A special technique was employed in studying individual gallery systems. The circumference of the block was marked in one-inch sectors, which were numbered in sequence from the dividing line between the first and the fourth quadrants. Ambrosia beetle entrance holes were numbered, and from each a transverse line was drawn in both directions to mark the plane of the gallery system. The identification number was repeated at close intervals along the transverse line so that the holes belonging to a marked gallery could be identified after the block was split into segments (Fig. 1). Each numbered gallery

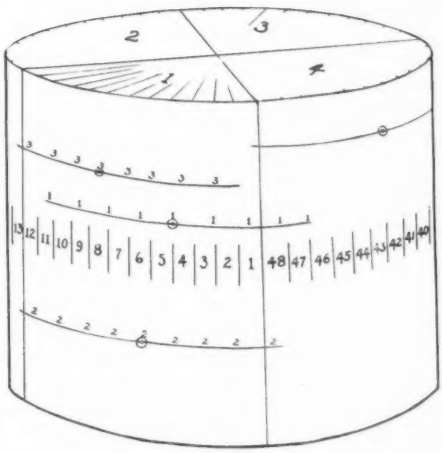

FIGURE 1. *Method of preparing sample block for analysis. Lines dividing the block into quarters are marked on the end, and extended along the sides of the block Short vertical lines divide the block into one-inch sectors, starting at the dividing line between quarters No. 1 and No. 4. Extensive transverse lines identify ambrosia beetle galleries selected for detailed individual study as the block is sectioned.*

was traced by splitting the block first into quarters, and then into one-inch sectors in the vicinity of the marked entrance holes; the depth of each gallery of the system was recorded for each sector in which it occurred. The use of a fine probe, for determining the end point of galleries and the presence or absence of the beetles, avoided much splitting of the sectors into successively finer pieces. About 20 individual gallery systems could be studied conveniently in any one block. These were distributed among the four quadrants and in different transverse planes in the block to avoid confusion.

The pattern of each gallery system so studied was reconstructed from the field data through the use of charts (Fig. 2). On the chart, pins were inserted at the appropriate depths in each sector according to the records obtained as the block was split. Measurements of lateral extent and

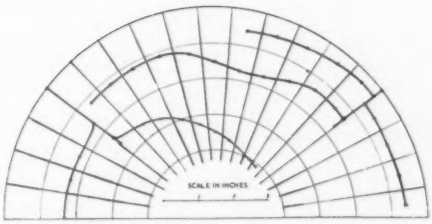

FIGURE 2. *Method of reconstructing individual gallery systems. Measurements of lateral extent and total gallery length are read from pin locations in the master chart, representing depth measurements of galleries made in one-inch sectors as the sample blocks are dissected.*

of the total length of the gallery system were read directly from this reconstruction. The gallery patterns made by the different species of ambrosia beetles were clearly portrayed in the reconstructions.

A direct measurement of damage was obtained by recording the number and depth of all holes appearing on each of about 20 radial sections, distributed among the four quarters of each block. Holes caused by different species of beetles were recorded separately.

In the compilation, the field data were segregated into groups based on tree species, period of felling, and time of examination. A further breakdown was made for rate of growth, according to the number of annual rings in the outer inch of wood in the Douglas fir logs, in which rate of growth was more variable than in the other species.

For each sample block the density of attack was computed separately for each species of beetle. Density of attack was expressed as number of entrance holes per square foot of wood surface, rather than bark surface, because in field examinations it is necessary to strip the bark to make an accurate count and to identify the entrance holes by species. Averages were computed separately for each log group referred to above.

The depth of holes appearing on radial sections of the sample blocks was measured in the field to the nearest 1/16 inch, but the compilations were simplified by use of the following depth classes (in sixteenths): 1–3, 4–6, 7–9,... 31–33; 34–40, 41–47, 48–54, 55–61, 62–68; 69–81, 82–94, etc. Totals for each class, and for all depths, were prepared for each sample block, and the average for the log group was expressed as the number of holes per linear foot of radial section.

Gallery Patterns

Representative gallery patterns reconstructed from the log dissection records are shown in Figures 3–6. Simplicity of pattern is characteristic of the galleries of *Xyleborinus tsugae* and *Trypodendron* spp., and increasing complexity of the well-developed galleries of *Gnathotrichus sulcatus* and *Platypus wilsoni.*

The transverse galleries of Trypodendron are frequently constructed very close to, and are sometimes visible from, the log surface. This habit appears to be related to high water content of the log. In Douglas fir, the galleries are restricted to the sharply defined sapwood, which varies in thickness from about ½ inch in old growth timber to 2½ inches in rapidly growing timber. In amabilis fir and western hemlock, the sapwood is not sharply differentiated from the heartwood, and Trypodendron galleries penetrate the latter, reaching depths of 4 inches or more from the log surface. The most extensive Trypodendron gallery system encountered in these studies had an expanse, between gallery tips, of 6 inches and a total length of 7 inches. Average values of these measurements were about 3, and 3½ inches, respectively.

A completed Gnathotrichus gallery system consists of the entrance gallery projected radially, and up to six transverse galleries at various depths, each essentially concentric with an annual ring. The maximum total length of gallery system en-

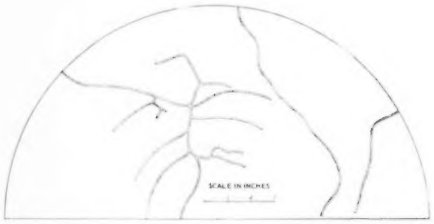

FIGURE 3. *Gallery patterns of* Platypus wilsoni.

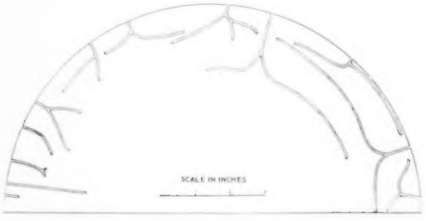

FIGURE 4. *Gallery patterns of* Trypodendron *spp.*

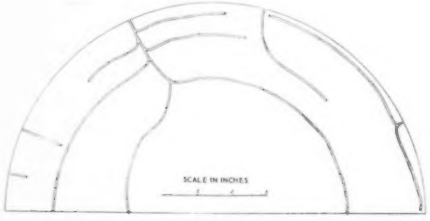

FIGURE 5. *Gallery patterns of* Gnathotrichus sulcatus.

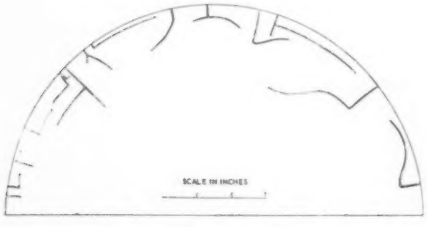

FIGURE 6. *Gallery patterns of* Xyleborinus tsugae.

countered in these studies was 29 inches. Sapwood thickness restricts the depth of penetration in Douglas fir, but not in amabilis fir and western hemlock.

Distribution of Attack

Time and intensity of attack may be quite variable in different logs from the same tree. Such variations are probably related to physiological conditions within the logs, including moisture content, which influence attractiveness to the beetles. Intra-log variability was not studied in this investigation, because the sampling and sectioning technique could not be applied at successive points in the valuable 40- to 60-foot logs available for study. Critical studies of the factors influencing incidence and distribution of ambrosia beetle attacks within and between logs should be carried out under strictly experimental conditions.

Attack is not entirely at random at any point in the length of a log. The data for Trypodendron and Gnathotrichus attacks in different quarters of the one-foot blocks sectioned in 1942 and 1943 are summarized in Table 1. In exposed logs, Trypodendron attack density was lowest in the most exposed quarter (no. 1). In shaded logs, attack density was approximately equal in all four quarters, except in amabilis fir where the sample was small. The number of Gnathotrichus attacks was too small for reliable conclusions, but the data suggest a concentration of attacks in the two quarters (no's. 2 and 3) in the lower half of the logs.

The combined data for all logs and exposure conditions show that about 52 per cent of the Trypodendron attack, and about 62 per cent of the Gnathotrichus attack, occurred in the lower half of the logs. Attacks by Platypus and Xyleborinus were too infrequent to permit any generalization.

Holes in Radial Sections

Estimation of the number of holes in radial sections is subject to considerable sampling error, owing to unequal distribution of attacks in different quarters of the log, and

TABLE 1. Summary of Trypodendron and Gnathotrichus attacks in 1942 and 1943 sample blocks.

	Trypodendron						Gnathotrichus					
	Exposed logs[3]			Shaded logs			Exposed logs			Shaded logs		
	D. fir	Hem.	A. fir	D. fir	Hem.	A. fir	D. fir	Hem.	A. fir	D. fir	Hem.	A. fir
No. of Sample blocks	128	141	45	38	62	50	128	141	45	38	62	50
Quarter 1[1]												
Attacks[2]	218	95	45	167	79	25	4	11	3	4	8	3
% of total	18.5	20.8	22.5	23.8	24.4	19.2	12.1	16.9	14.3	21.0	12.3	18.8
Quarter 2												
Attacks	340	122	47	162	96	31	9	20	7	6	21	6
% of total	28.8	26.8	23.5	23.0	29.6	23.9	27.3	30.8	33.3	31.6	32.3	37.5
Quarter 3												
Attacks	333	126	49	198	70	36	14	20	7	3	23	4
% of total	28.2	27.6	24.5	28.2	21.6	27.7	42.4	30.8	33.3	15.8	35.4	25.0
Quarter 4												
Attacks	290	113	59	176	79	38	6	14	4	6	13	3
% of total	24.5	24.8	29.5	25.0	24.4	29.2	18.2	21.5	19.1	31.6	20.0	18.8
Total attacks	1181	456	200	703	324	130	33	65	21	19	65	16

[1]Quarter 1 of each block was in the top half and in the most exposed location; the remaining quarters were in clockwise sequence.

[2]The number of attacks per quarter is the total of attack densities per square foot, for all blocks in the series.

[3]Exposed logs were moderately to fully exposed; shaded logs were moderately to heavily shaded by surrounding logs or trees.

to variation in gallery construction. Data for Trypodendron attack, based on 20 radial sections per block, and representative of the range of variability in attack density in the three tree species, are summarized in Table 2. Variability in the number of holes in radial sections was great in sample blocks with less than ten Trypodendron attacks per square foot, but was markedly reduced at the higher densities of attack. More ex-

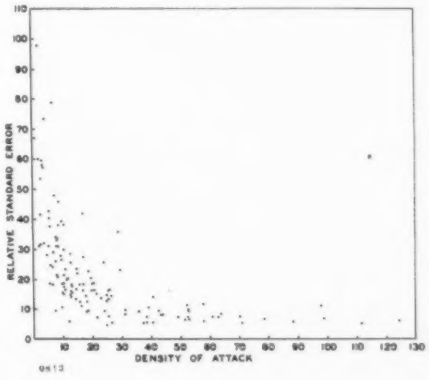

FIGURE 7. *Standard error of the mean number of holes in radial sections as a percentage of the mean (relative standard error) plotted against density of attack of* Trypodendron *spp. in all log species.*

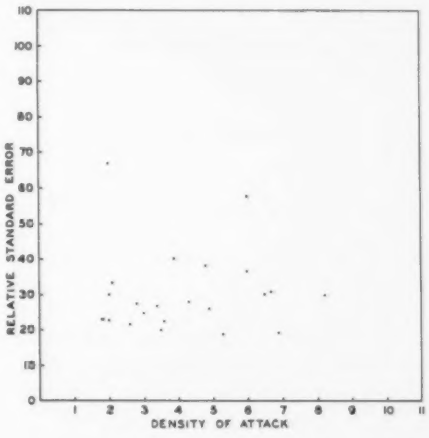

FIGURE 8. *Standard error of the mean number of holes in radial sections as a percentage of the mean (relative standard error) plotted against density of attack of* Gnathotrichus *in all log species.*

TABLE 2. Variability in number of Trypodendron holes in radial sections of representative logs.

Block No.	Density of attack[1]	Holes in radial sections Mean[2]	S.D.[3]	C.V.[4]	S.E.[5]	Rel. S.E.[6]	Sample size[7]
Douglas fir							
435	0.25	0.05	0.22	440	0.049	99	2000
277	2.5	0.40	0.75	187	0.165	41	356
273	5.2	0.70	0.97	138	0.217	31	196
360	10.2	1.00	1.70	170	0.380	38	289
596	16.0	4.60	2.30	50	0.514	11	25
556	25.4	9.00	3.11	35	0.695	8	12
415	51.3	14.90	4.33	29	0.968	6	8
421	78.4	22.20	6.87	31	1.536	7	10
418	124.5	31.55	8.63	27	1.919	6	7
213	261.0	26.25	6.21	24	1.380	5	6
Western hemlock							
424	0.6	0.10	0.30	300	0.067	67	900
131	2.3	0.35	0.49	140	0.110	31	196
204	5.2	0.30	0.57	190	0.128	43	370
72	10.1	2.70	2.10	78	0.470	17	61
87	15.7	4.40	3.22	73	0.720	16	53
408	44.0	6.10	2.20	36	0.492	8	13
202	97.7	10.85	6.14	57	1.373	13	32
Amabilis fir							
397	2.7	0.15	0.36	240	0.080	53	578
77	4.5	1.00	1.26	126	0.282	28	158
577	10.9	3.00	3.18	106	0.711	24	112
84	17.7	5.30	2.15	41	0.481	9	16
410	24.0	6.50	3.40	52	0.759	12	27
412	35.7	7.35	3.51	48	0.785	11	23
350	40.8	3.55	2.19	62	0.490	14	39

[1]Entrance holes per square foot of log surface.
[2]Holes per linear foot of radial section, based on 20 sections for the 1-foot block.
[3]Standard deviation.
[4]Coefficient of variation, to nearest integer.
[5]Standard error of the mean number of holes.
[6]Relative standard error (standard error as percentage of mean) to nearest integer.
[7]Number of radial sections required to yield a mean whose standard error will not exceed 10 percent of the mean. $\left[n = \left(\frac{\text{S.D.}}{.10\ (\text{mean})}\right)^2\right]$

tensive data on the relationship of variability in Trypodendron holes in radial sections to density of attack are shown in Figure 7. Comparable data for Gnathotrichus are shown in Figure 8.

It is difficult to achieve precision in estimating number of holes per foot of radial section, at low attack densities. If the aim were to keep the standard error of estimate within 10 per cent of the mean number of holes per foot of radial section, more than 100 sections would be required in each sample block at low attack densities (Table 2). However, not more than about 20 radial sections can be examined in a block of moderate diameter without obtaining merely a succession of sections penetrated by the same beetle galleries. Variability might be less if the sample unit were a section two or three feet long, but blocks of such length would be difficult to handle and to dissect manually under field conditions.

Damage Indices

Damage to infested logs, expressed in terms of the number and depth of holes appearing in radial sections, will increase with the density of attack, the depth of penetration, and the progressive lateral ex-

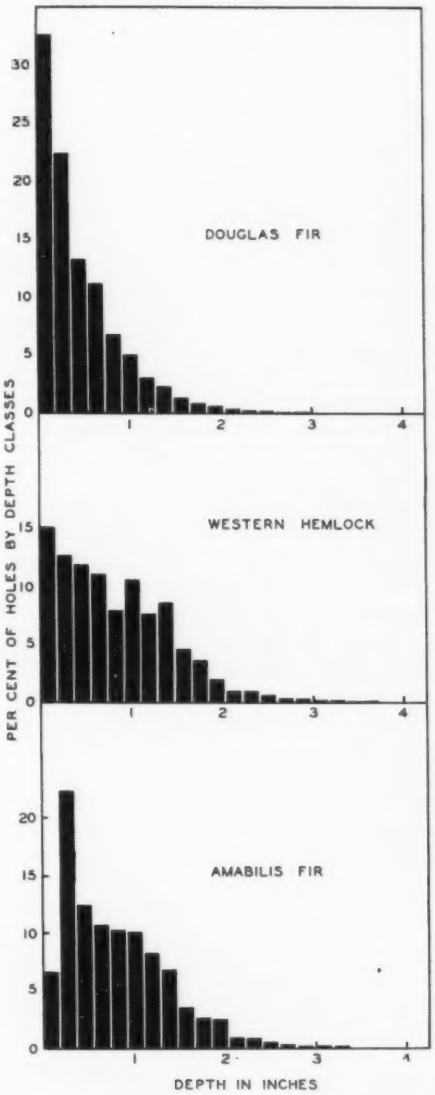

FIGURE 9. *Distribution of* Trypodendron *holes by depth classes in radial sections of Douglas fir, western hemlock, and amabilis fir logs.*

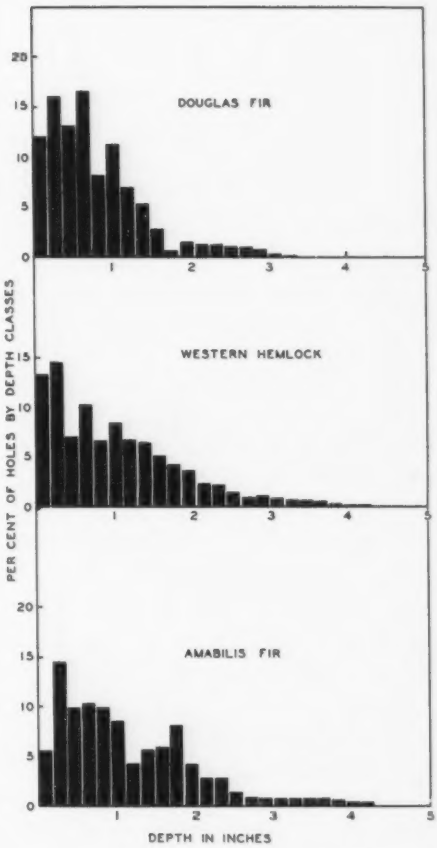

FIGURE 10. *Distribution of* Gnathotrichus *holes by depth classes in radial sections of Douglas fir, western hemlock, and amabilis fir logs.*

tension of the gallery system. One of the first requirements of a damage index is reasonable consistency in the distribution of holes at different depths in the wood. Frequency histograms of Trypodendron holes in logs examined in this study are shown in Fig. 9. Similar histograms of Gnathotrichus holes are shown in Fig. 10. The deeper penetration of Gnathotrichus is apparent in the three species of logs, and both species of beetles penetrate deeper in western hemlock and amabilis fir than they do in Douglas fir. The proportions of the holes found at different depths in this study, and in slabs in a mill study conducted by Graham *et al.* (1950), are shown in Table 3. Trypodendron holes were

TABLE 3. Approximate cumulative percentages of total holes at successive depths in the wood.

	Depth from outside of log (inches)				Greatest depth (inches)
	½	1	1½	2	
Trypodendron					
Douglas fir	62	88	97	99	2.7
Douglas fir[1]	80	97	100	—	1.3
Western hemlock	34	63	86	95	3.6
Western hemlock[1]	48	75	91	98	4.4
Amabilis fir	35	66	89	96	3.2
Gnathotrichus					
Douglas fir	33	68	88	93	3.2
Western hemlock	31	55	74	86	5.3
Amabilis fir	25	53	69	86	4.2

[1]Data from mill study by Graham, Kinghorn, and Webb (1950). All other data in the table are drawn from field analyses of sample blocks.

Note. The cumulative percentages for the data drawn from sample blocks are approximate, rather than exact, because the depth classes adopted in compilation (see Methods) did not divide exactly at ½, 1 or 2 inches. The frequencies in the classes overlapping these particular depths were prorated.

very similarly distributed in western hemlock and amabilis fir sample blocks. The distribution of Gnathotrichus holes was also closely similar in these two logs species. However, quite marked differences are apparent in the distribution of holes made by both species of beetles in Douglas fir, in comparison with hemlock and amabilis fir; and in the distribution of Trypodendron holes in Douglas fir and hemlock slabs examined in the mill study, in comparison with blocks of the same species studied in the field. Differences in the distribution of holes in Douglas fir are not unexpected, owing to the influence of growth rate and sapwood thickness on penetration of the beetles. The data in Table 4, from adjacent Douglas fir logs felled in October 1941 and analyzed at mid-September 1942, illustrate this feature. Variations of the magnitude shown in Tables 3 and 4 indicate that depth of penetration, and distribution of holes by depth classes, are not predictable with a high degree of precision.

Gallery systems, taken at random, were studied in many logs. From the individually reconstructed gallery patterns, the average depth of penetration, the average lateral extent of each gallery (measured between the extremities of its branches), and the average total length of gallery system were calculated for Trypodendron and Gnathotrichus in each log thus studied. Such data, along with density of attack and the number of holes in radial sections, are available for Trypodendron attacks in 75 Douglas fir, 62 western hemlock, and 38 amabilis fir logs; and for Gnathotrichus attacks in 40 Douglas fir, 81 western hemlock, and 22 amabilis fir logs. Representative data, to illustrate the range of conditions from the lightest to the heaviest attack and damage encountered, are shown in Table 5. Increase in number of holes per foot of radial section is associated with

TABLE 4. Percent of holes at different depths for Trypodendron and Gnathotrichus.

	Trypodendron Cumulative percent of holes at different depths					*Gnathotrichus* Cumulative percent of holes at different depths				
	0.5″	1″	1.5″	2″	2.5″	0.5″	1″	1.5″	2″	2.5″
Logs with moderate growth rate, 22 rings per outer inch	32	63	85	95	99.6	0	43	100	–	–
Logs with very slow growth rate, 90 rings per outer inch	82	100	–	–	–	57	100	–	–	–

TABLE 5. Data for representative sample blocks, showing density of attack, average gallery measurements, and number of holes in radial sections.

Block No.	Density of attack[1]	Average gallery measurements[2] Depth	Lat. extent	Total length	Holes in radial sections[3]
Trypodendron					
Douglas fir					
197	1.5	14	13	26	.10
48	3.8	10	54	73	1.83
255	12.8	5	50	61	4.60
415	51.3	4	60	64	14.90
215	98.5	21	31	54	23.00
213	261.0	20	10	28	26.25
Western hemlock					
303	1.6	7	2	9	.10
425	3.5	23	45	68	.75
427	12.7	22	36	58	3.60
367	52.1	19	18	37	6.15
202	97.7	26	20	46	10.85
Amabilis fir					
397	2.7	10	12	22	.15
123	4.8	18	36	54	1.05
78	9.8	14	21	38	2.87
410	24.0	21	44	65	6.50
350	40.8	20	12	30	3.55
Gnathotrichus					
Douglas fir					
495	1.5	17	39	54	.45
71	5.0	9	60	77	2.12
47	10.0	22	127	179	5.61
Western hemlock					
388	1.3	10	0	10	.05
20	3.8	26	92	144	3.50
198	7.2	46	64	121	5.45
97	10.8	22	37	72	3.70
Amabilis fir					
58	1.3	4	13	17	.17
208	3.6	38	55	108	2.35
123	6.9	15	27	45	3.30

[1]Entrance holes per square foot.
[2]Measurements in sixteenths of inches.
[3]Number of holes per foot of radial section.

increase in density of attack and extent of gallery construction. The mass of data, of which Table 5 is representative, provides the basis for correlation of damage with various measures of attack and gallery development.

The correlation of number of holes in radial sections with density of attack is shown in the top panel of Table 6. All values of r are significant[4] (P less than

[4]Significance of r by the t test,

$$t = \frac{r\sqrt{n}}{\sqrt{1-r^2}}.$$

Significance of differences between values of r tested by the z transformation,

$$t = \frac{z_1 - z_2}{\text{S.D.}_{(z_1 - z_2)}}.$$

TABLE 6. Correlation of number of holes in radial sections with measurements of attack and galley development.

Correlated variables	Log species	Trypodendron		Gnathotrichus	
		N[1]	r^2	N	r
Holes in radial sections	Douglas fir	75	.856	40	.622
with	W. hemlock	62	.909	81	.751
Density of attack	Amabilis fir	38	.752	22	.903
Holes in radial sections	Douglas fir	58	.958	26	.981
with	W. hemlock	58	.931	61	.914
Density of attack x average lateral extent of galleries	Amabilis fir	37	.961	20	.943
Holes in radial sections	Douglas fir	75	.982	39	.976
with	W. hemlock	62	.938	81	.949
Density of attack x average total length of galleries	Amabilis fir	38	.972	22	.951

[1]Number of one-foot blocks in sample.

[2]Correlation coefficient.

.01), and significant differences in r occur between the following pairs:

Trypodendron in western hemlock and amabilis fir

Gnathotrichus in Douglas fir and amabilis fir

Gnathotrichus in western hemlock and amabilis fir

Trypodendron and Gnathotrichus in Douglas fir

Trypodendron and Gnathotrichus in western hemlock.

In view of the more prolonged period of attack and gallery construction in Gnathotrichus, it was rather unexpected that correlation of holes in radial sections with density of attack should be nearly as strong in this species as in Trypodendron, which has concentrated attacks and rapid gallery development.

Since r^2 defines the proportion of variation in one variable attributable to variation in the other variable, it follows that from 57 to 83 percent (average 71 percent) of the variation in Trypodendron holes in radial sections is directly attributable to variations in the density of attack in the sample blocks. In the Gnathotrichus infestations the corresponding range in the three log species is 39 to 82 per cent (average 59 percent).

Regression equations for estimation of number of holes in radial sections (Y) from the density of attack (X), based on the six series, follow.

Trypodendron

Douglas fir

$$Y = .9915 + .1642\ X$$

western hemlock

$$Y = .1117 + .1254\ X$$

amabilis fir

$$Y = -.0588 + .1580\ X$$

Gnathotrichus

Douglas fir

$$Y = .0106 + .2206\ X$$

western hemlock

$$Y = -.0915 + .4296\ X$$

amabilis fir

$$Y = -.1874 + .4979\ X$$

All regression coefficients are highly significant[5] (P less than .01). Significant dif-

[5]Significance of b_{yx} by the t test,

$$t = \frac{b_{yx}\sqrt{\Sigma\,(x-\bar{x})^2}}{\sqrt{\frac{\Sigma\,(y-Y)^2}{N-2}}}.$$

Significance of differences between values of b_{yx} tested as follows:

$$t = \frac{b_1 - b_2}{\sqrt{(S.E._1)^2 + (S.E._2)^2}}.$$

ferences in the regression coefficient occur between the following pairs:

Trypodendron in Douglas fir (.1642) and western hemlock (.1254)
Gnathotrichus in Douglas fir (.2206) and western hemlock (.4296)
Gnathotrichus in Douglas fir (.2206) and amabilis fir (.4979)
Trypodendron (.1254) and Gnathotrichus (.4296) in western hemlock
Trypodendron (.1580) and Gnathotrichus (.4979) in amabilis fir.

The principal differences in the regression coefficient occur between Trypodendron and Gnathotrichus infestations. This follows naturally from the more complex gallery pattern of Gnathotrichus. Normally there will be more holes per foot of radial section in Gnathotrichus infestations than in Trypodendron infestations of the same density of attack.

The sigificantly lower regression coefficient for Gnathotrichus in Douglas fir (.2206) than in western hemlock and amabilis fir (.4296 and .4979, respectively) reflects conditions in the sample of Douglas fir logs, and is probably not characteristic of Gnathotrichus attack in this species. About one-third of the Douglas fir logs were sectioned shortly after attack, when only the radial component of the gallery had been constructed. Furthermore, three sample logs had high attack densities but little gallery development, and hence few or no holes in radial sections. Because of their large contribution to the sum of squares (X), and minor contribution to the sum of cross-products (XY), these sample units greatly reduced the regression coefficient. Omitting the three blocks from the sample would yield a regression coefficient of approximately .438, very similar to those for Gnathotrichus in western hemlock and amabilis fir.

Another illustration of the influence of conditions within sample logs upon estimation of holes in radial sections from the density of attack, is afforded by differences between regression coefficients for Trypodendron obtained in this study, and those recorded by Graham *et al.* (1950). Here the coefficients for Douglas fir and western hemlock are .1642 and .1254, respectively, in contrast with values of .220 and .240 recorded by Graham *et al.*

Since the extent of gallery construction influences the number of holes in radial sections, it is reasonable to expect that the number of holes would be more strongly correlated with a combination variable, embodying some measure of gallery construction as well as density of attack. Two analyses were carried out. In the first, density of attack (number of entrance holes per square foot of log surface) was multiplied by the average distance between extremities of the gallery system (in sixteenths of inches) to form the independent variable. The correlation coefficients are shown in the middle panel of Table 6. The number of blocks in the sample series is reduced by elimination of those in which the galleries had no lateral component and in which there were no holes in radial sections. Such blocks, in which both X and Y equal 0, make no contribution to the sums of squares and cross-products. All values of r are highly significant (P less than .01), but the only significant differences within the series are between $r = .981$ for Gnathotrichus in Douglas fir, and $r = .914$ and $r = .931$ for Gnathotrichus in western hemlock and Trypodendron in western hemlock, respectively.

The incorporation of the measurement of lateral extent of the galleries into the independent variable increased r in all cases (compare corresponding values in top and middle panels of Table 6). All increases in r are significant except for Trypodendron in western hemlock and Gnathotrichus in amabilis fir, where r, based on density alone, is over 0.9. With r averaging about 0.95 in the middle panel of Table 6, it is evident that about 90 percent of the variation in number of holes in radial sections is accounted for by density of beetle attack and the progress of gallery construction as expressed by the average distance between extremities of gallery sys-

tems in the log.

The distance between extremities of a gallery system does not necessarily provide the best measurement of gallery development. This measurement takes no account of separate branches of the gallery system, at successive depths. However, each branch of the system is represented by a hole in a radial section passing through the gallery system. Therefore, in the second analysis of combination independent variables, density of attack was multiplied by the average total length of the gallery systems in each sample block. Measurements of total length were taken from reconstructed gallery systems as described earlier. Resulting correlation coefficients are shown in the bottom panel of Table 6. In all but one case (Gnathotrichus in Douglas fir) there is an increase in r over the corresponding values in the middle panel; however, in an instance is the difference in r significant. With r averaging about 0.96 in the bottom panel of Table 5, it is evident that about 92 per cent of the variation in number of holes in radial sections is directly attributable to the density of attack and the average total length of gallery systems in the log.

Although combination of gallery measurements with density of attack leads to more precise correlation with number of holes in radial sections than the use of density of attack alone, it would be impractical to use such combination variables as the basis of estimation of damage within the log. It is a more time-consuming task to obtain representative measurements of gallery development within the log than to record, directly, the number of holes in radial sections. Where it is important to have an estimate of existing or potential damage and it is inconvenient or uneconomic to section sample blocks, the density of attack will permit an estimate of the number of holes per foot of radial section, employing regression equations referred to earlier. However, as already indicated, the regression coefficient for a given combination of beetle species and log species is not invariable, but tends to reflect conditions of gallery development in the sample logs. Moreover, there will be variations in the depth of penetration, and in the distribution of holes by depth classes, that cannot be predicted with precision.

Influence of Time of Felling

Qualitative records of ambrosia beetle attack in western hemlock logs felled at monthly intervals have been reported by Mathers (1935). Fellings were made near Mission, B.C., over a 24-month period starting in July, 1932, and new attacks were recorded monthly until the end of the 1935 season. The following conclusions are drawn from these systematic observations:

1. Trypodendron attacks occurred predominantly in April and to a lesser extent in May-July, in hemlock logs felled 5 to 20 months previously. Logs felled after December were not attacked by Trypodendron until the second season of exposure.
2. Gnathotrichus attacks occurred from April to August in hemlock logs felled as recently as one week before attack. Some logs felled in January were attacked in both the first and second seasons of exposure; others escaped attack the first season, but were attacked in the second and third seasons of exposure.
3. Platypus attacks occurred in July and August. Some of the attacked hemlock logs had been felled within the month preceding attack. Several of the logs were attacked by Platypus during two consecutive seasons. Some logs felled in January escaped Platypus attack during the first season of exposure, but were attacked in the second and third seasons.
4. All hemlock logs in the series were eventually attacked during two consecutive seasons. Half of the logs were attacked by only two species, and the other half by all three species of beetles.

The records of attack in relation to felling date, on Vancouver Island, lack the continuity of observations recorded by Mathers. There are many gaps in the series due to unavailability of logs felled in a given month, and impossibility of analyzing samples at consecutive monthly periods.

The quantitative records of density of attack, and the extension of sampling to logging operations in several parts of Vancouver Island, partially compensate for gaps in the series. The data are summarized in Tables 7 to 11

tables, it should be kept in mind that each entry in any one cell represents a separate series of logs, distinct as to species, location, or year of felling; secondly, that a series of diagonal lines extending from the lower left to the upper right establishes equivalent calendar months when analyses were carried out in the field; and thirdly, except for the analyses in the first month after felling, the results of log analyses do not establish the time when attack occurred. In studies carried out by this method, the time of attack can only be deduced from knowledge of beetle biology, and from consistency in the body of data.

The principal conclusions drawn from these compilations are summarized first by beetle species, and then by "hazard" to logs of the different species, in relation to felling date.

Trypodendron

This beetle made the heaviest attacks, ranging as high as 261 entrances per square foot in individual logs, with averages up to 65 per square foot for the logs of a sample series. Attacks were made principally in April and May, and were heaviest in logs felled in October to December. Attacks were usually much lighter in logs felled from January to May. The records of attack during the first seven months of exposure in logs felled from March to May (Table 7) applied mostly to Douglas fir; in equivalent series, western hemlock logs were entirely free of attack, and amabilis fir logs nearly so. Except for very minor attack in one series of Douglas fir logs, June to August fellings were free of Trypodendron attacks until the following year.

Our records indicate a wider range of attack by Trypodendron than do Mathers' observations. It has already been noted that Douglas fir logs are more susceptible than hemlock and amabilis fir. Douglas fir logs felled from January to May were attacked, moderately to heavily, by Trypodendron during its first flight period. Western hemlock logs felled in January were moderately attacked by Trypodendron during its first flight period, but fellings in April or later were not attacked until the following year. Attacks in amabilis fir were similar to those in hemlock, except for early light attack by Trypodendron in a few series of logs felled in April.

Gnathotrichus

Attacks by this species were not so heavy as those of Trypodendron. The highest density of attack recorded in any single log was 10.8 entrances per square foot of log surface, and the highest average for any sample series was 7.9. Attacks occurred in May, but were more common in June, July or August. The data (Table 8) give little evidence of concentration of attack in logs of any of the three tree species, or in logs of a particular felling period. The absence of attack in September fellings, representing all three tree species, was probably fortuitous. It was not supported by results in August and October fellings; nor do Mathers' records suggest any reduced susceptibility in September fellings.

One point of contrast between our records and those obtained by Mathers concerns the freshness of logs attacked by Gnathotrichus. Mathers (1935) observed some attacks in western hemlock logs within a week of felling, and consistent attacks within the first month after felling in March to July, inclusive. In our studies, there was no attack in seven log series felled from May to August and examined within a month of felling. Among 15 log series felled from March to July, and examined in the second month after felling, logs of only five series were attacked.

Platypus

This species was encountered in six series of western hemlock logs, in one series of amabilis fir logs, and not at all in Douglas fir logs. The maximum average density of attack in any log series was 0.26 entrances

TABLE 7. Trypodendron attack in relation to felling date and period of exposure.

Each entry in the table is the average number of attacks per square foot of log surface for a series of logs of any one tree species. Number of attacks to nearest one-tenth; trace (T) indicates less than 0.05 per square foot. A dash indicates no data are available. Log analyses were made from late May to late November, but not from December to April, inclusive.

Month of felling	Period of examination (months of exposure after felling date)														
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
April	—	0, 0, 1.1 0, 0, 2.8	0, .5, 1.4 0, .8, 8.2	0, .6 .6	0, 0 0	—	0	—	—	—	—	—	—	—	0
May	0, 12.4 1.3	0, 39.1 3.5	—	0, 0 0	—	—	—	—	—	—	—	0, .8 .6, 4.7	2.4 6.6	.6, 5.9 1.6, 15.3	—
June	0 0	0, .3 0	0, 0 0	— —	0, 0 0	—	—	—	—	—	—	—	—	—	—
July	0	0	—	0 0	—	—	—	—	—	11.7	2.5, 15.9 13.2	11.8 15.4	—	—	—
August	0 0	—	—	—	—	—	—	—	—	T	6.8	—	—	—	—
September	—	—	—	—	—	—	—	0	1.1, 5.1 3.3, 8.6	0 9.0	—	—	—	—	—
October	—	—	—	—	—	—	9.8	—	—	—	12.2, 41.4 16.4, 65.6	—	—	—	—
November	—	—	—	—	—	—	40.3	—	—	—	—	12.8	—	—	—
December	—	—	—	—	—	12.2, 61.3 56.1	12.3, 39.8 22.6, 63.0	—	—	—	—	—	—	—	—
January	—	—	—	10.7 12.1	0, T, 3.4 0, 2.4, 7.3	—	—	—	—	—	—	—	—	—	—
February	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
March	—	0 6.9	—	0	—	—	—	—	—	—	—	—	—	—	—

TABLE 8. Gnathotrichus attack in relation to felling date and period of exposure.

Each entry in the table is the average number of attacks per square foot of log surface for a series of logs of any one tree species. Number of attacks to nearest one-tenth; trace (T) indicates less than 0.05 per square foot. A dash indicates no data are available. Log analyses were made from late May to late November, but not from December to April, inclusive.

Month of felling	Period of examination (months of exposure after felling date)														
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
April	—	0, 0, 0 0, 0, .2	T, .8, 1.4 .3, .9, 7.9	.1, 2.2 1.5	.1, .8 .4	—	T	—	—	—	—	—	—	—	3.2
May	0, 0 0	0, .3 0	— —	.1, .2 .2	— —	— —	— —	— —	— —	— —	— —	0, 1.6 .1, 2.2	.1 .6	0. 1.0 .4, 2.3	— —
June	0 0	0, 3.9 0	T, .4 .4	— —	0, .2 .2	— —	— —	— —	— —	— —	— —	— —	— —	— —	— —
July	0	0	—	0 .1	—	—	—	—	—	.9	0, T .6	2.0 1.3	—	—	—
August	0	—	—	—	—	—	—	—	—	3.4	2.5	—	—	—	—
September	—	—	—	—	—	—	—	0	0, 0 0, 0	0 0	—	—	—	—	—
October	—	—	—	—	—	—	0	—	—	—	.4, 1.6 .5, 3.4	—	—	—	—
November	—	—	—	—	—	—	.1	—	—	—	—	.7	—	—	—
December	—	—	—	—	—	0, 0 0.	.1, .3 .1, 1.4	—	—	—	—	—	—	—	—
January	—	—	—	0 0	0, 0, .2 0, T, .2	—	—	—	—	—	—	—	—	—	—
February	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
March	—	T .3	—	.7	—	—	—	—	—	—	—	—	—	—	—

TABLE 9. Total attacks by all species of Ambrosia beetles in relation to felling date and period of exposure. Douglas fir.

Each entry in the table is the average total number of attacks per square foot of log surface for one series of sample blocks. Number of attacks to nearest one-tenth; trace (T) indicates less than 0.05 per square foot. A dash indicates no data are available. Log analyses were made from late May to late November, but not from December to April, inclusive.

Month of felling	Period of examination (months of exposure after felling date)													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
April	—	1.1 2.8	2.8 16.0	2.8	.4	—	—	—	—	—	—	—	—	—
May	1.3 12.4	3.5 39.4	—	.2	—	—	—	—	—	—	—	.1, 2.8 .8	—	1.6 17.6
June	0	0 4.2	.4	—	.2	—	—	—	—	—	—	—	—	—
July	0	—	—	0	—	—	—	—	—	—	15.9	—	—	—
August	0	—	—	—	—	—	—	—	—	3.6	—	—	—	—
September	—	—	—	—	—	—	—	—	1.1 5.1	9.0	—	—	—	—
October	—	—	—	—	—	—	9.8	—	—	—	41.9 66.0	—	—	—
November	—	—	—	—	—	—	40.7	—	—	—	—	13.6	—	—
December	—	—	—	—	—	61.3	23.9 63.1	—	—	—	—	—	—	—
January	—	—	—	12.2	0 7.7	—	—	—	—	—	—	—	—	—
February	—	—	—	—	—	—	—	—	—	—	—	—	—	—
March	—	T 7.2	—	.7	—	—	—	—	—	—	—	—	—	—

TABLE 10. Total attacks by all species of Ambrosia beetles in relation to felling date and period of exposure. Western hemlock.

Each entry in the table is the average total number of attacks per square foot of log surface for one series of sample blocks. Number of attacks to nearest one-tenth; trace (T) indicates less than 0.05 per square foot. A dash indicates no data are available. Log analyses were made from late May to late November, but not from December to April, inclusive.

Month of felling	Period of examination (months of exposure after felling date)														
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
April	—	0 .2	.3 .9	1.5	1.0	—	T	—	—	—	—	—	—	—	3.3
May	—	—	—	.3	—	—	—	—	—	—	—	6.5	6.8	1.6 6.5	—
June	0	0	.4	—	.2	—	—	—	—	—	—	—	—	—	—
July	—	0	—	.1	—	—	—	—	—	12.5	2.5	13.8	—	—	—
August	0	—	—	—	—	—	—	—	—	—	16.1	—	—	—	—
September	—	—	—	—	—	—	—	0	3.3	0	—	—	—	—	—
October	—	—	—	—	—	—	—	—	—	—	20.1	—	—	—	—
November	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
December	—	—	—	—	—	56.1	39.9	—	—	—	—	—	—	—	—
January	—	—	—	10.7	T 4.2	—	—	—	—	—	—	—	—	—	—
February	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
March	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—

TABLE 11. Total attacks by all species of Ambrosia beetles in relation to felling date and period of exposure. Amabilis fir.

Each entry in the table is the average total number of attacks per square foot of log surface for one series of sample blocks. Number of attacks to nearest one-tenth; trace (T) indicates less than 0.05 per square foot. A dash indicates no data are available. Log analyses were made from late May to late November, but not from December to April, inclusive.

Month of felling	Period of examination (months of exposure after felling date)												
	1	2	3	4	5	6	7	8	9	10	11	12	13
April	—	0 0	.8 1.3	.7	.1	—	—	—	—	—	—	—	—
May	0	0	—	.3	—	—	—	—	—	—	—	—	3.0
June	—	—	T	—	0	—	—	—	—	—	—	—	—
July	—	—	—	—	—	—	—	—	—	—	13.7	16.7	—
August	—	—	—	—	—	—	—	—	—	—	—	—	—
September	—	—	—	—	—	—	—	—	8.6	—	—	—	—
October	—	—	—	—	—	—	—	—	—	—	13.8	—	—
November	—	—	—	—	—	—	—	—	—	—	—	—	—
December	—	—	—	—	—	12.2	12.6	—	—	—	—	—	—
January	—	—	—	—	0 2.8	—	—	—	—	—	—	—	—
February	—	—	—	—	—	—	—	—	—	—	—	—	—
March	—	—	—	—	—	—	—	—	—	—	—	—	—

per square foot of log surface. Attacks occurred in late summer in logs that had been felled as recently as June of the year of attack.

The extended life cycle of this species is a deterrent to the build-up of large populations in logging operations. With continuation of the trend toward early removal of logs from the woods, damage by this species should cease to be a factor of any importance.

Xyleborinus

This species was also of infrequent occurrence. Attacks were recorded in six series of Douglas fir logs, five series of western hemlock logs, and two series of amabilis fir logs. The maximum average density of attack was 6.84 entrances per square foot of log surface in one series of hemlock logs, but this was exceptional; in other infested log series, the density of attack ranged from 0.02 to 0.61 entrances per square foot. Attacks were made in May and later, in logs that had been felled from August of the previous year until May of the year of attack. Because of its shallow depth of penetration and infrequent occurrence, this species of ambrosia beetle is not a serious factor in deterioration of logs in British Columbia. However, it attracted considerable attention in the export trade to Australia in the late 1920's and early 1930's (see Graham and Boyes, 1950).

Hazard to Douglas Fir

October, November, and December fellings were consistently the most heavily attacked, if left in the woods until the following May or June. Fellings made in January to May experienced moderate, or occasionally heavy, attacks during the first beetle flights. June fellings either escaped attack, or at most experienced light attack during the first summer. July and August fellings were not attacked until the following summer (Table 9).

Hazard to Western Hemlock

The heaviest attacks were recorded in logs felled in October and December, and left in the woods until the following June or later. Logs felled in January were moderately attacked in May. Unfortunately the series included no fellings in February and March (Table 10). Logs felled in April to August were attacked only lightly during the first summer, or escaped attack until the following May or June, when moderate attacks were experienced.

Hazard to Amabilis Fir

The series of fellings of amabilis fir left many gaps (Table 11). Logs felled in April to June were attacked only lightly, or not at all, during the first season of exposure. But early summer fellings, along with those of July to January, were moderately to heavily attacked if left in the woods until the following May or June.

Risk of injury is therefore low in hemlock and amabilis fir logs felled in May or later, and in Douglas fir logs felled in June or later, provided the logs can be removed from the woods before the beetle flights of the following year. These may be experienced from the end of March in very early seasons, or from early May in retarded seasons.

Summary and Conclusions

1. Five or more species of ambrosia beetles attack softwood logs in the coastal area of British Columbia, and cause degrade of the infested logs and the products manufactured from them. The species encountered in these studies are *Platypus wilsoni* Swaine, *Trypodendron lineatum* (Oliver), *Gnathotrichus sulcatus* Lec., *Gnathothrichus retusus* Lec., and *Xyleborinus tsugae* Swaine. Only *T. lineatum* and *G. sulcatus* were consistently present in the study material. However, other species of the genus Trypodendron occur in the area and may have been partially responsible for damage attributed to Trypodendron spp.

2. The investigations were undertaken to determine whether intensity of attack by the different species of beetles could be related to the time of felling of the logs and to the period of exposure. Resultant damage in the log was measured, and various indices of damage were investigated.

3. Sample blocks of 630 logs of Douglas fir, western hemlock, and amabilis fir were sectioned from 1942 to 1945. These comprised 96 lots representing different combinations of felling and examination dates. Each block was stripped of bark, attack density of each species of beetle was determined, and the block was sectioned radially to provide a measure of damage. The progress of gallery construction was studied in detail in about one-third of the sample blocks.

4. Density of attack varied greatly with time of felling, period of exposure, timber species, beetle species, among different logs from the same tree, and to some extent within the same log. Serious study of intra- and inter-log variability was precluded by limitation of the sectioning technique to the end of valuable 40- to 60-foot logs in commercial logging operations. At any one point in a log, attack by Trypodendron and Gnathotrichus tended to be heavier in the shaded portions of the log.

5. The number of holes appearing in radial sections is significantly correlated with the density of attack in Trypodendron and Gnathotrichus infestations. The degree of correlation is strengthened if allowance be made for the extent of gallery development as well as the density of attack.

6. An appropriate measure of damage

in infested logs should consider the depth as well as the number of holes in radial sections. However, depth of holes is not determined by density of attack, nor is it a fixed charcteristic of the beetles. The depth of penetration and the distribution of holes by depth classes appear to be influenced by certain characteristics of the attacked logs, including growth rate, moisture content, and the depth of sapwood in the case of Douglas fir. It is doubtful whether density of attack alone, or density of attack in combination with measurements of gallery development, will have practical value as indices of damage in log series whose characteristics do not necessarily conform with those of logs in which detailed basic studies are made. If it is important to estimate damage in a given situation, direct enumeration of the number and depth of holes in radial sections of sample blocks can be made readily, ignoring density of attack and details of gallery development. In other situations, e.g. in appraisal of influence of felling time or of insecticidal applications, it may suffice to have an estimate of density of attack, by comparative counts of entrances per unit length or unit area of the logs, ignoring depth of penetration and details of gallery development. However, in evaluating the effects of certain insecticides, it may be necessary to know whether gallery development has proceeded normally (Kinghorn, 1955).

7. Each of the species of ambrosia beetles has fairly distinctive and consistent patterns of attack in relation to season and felling date. Risk of damage is low in hemlock and amabilis fir logs felled in May or later, and in Douglas fir logs felled in June or later, provided that the logs are removed from the woods before the end of March of the following year.

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